



**STUDIES ON THE STRUCTURE AND ACTIVITY OF  
VASCULAR CAMBIUM IN ACACIA NILOTICA VAR.  
TELIA AND PROSOPIS SPICIGERA**

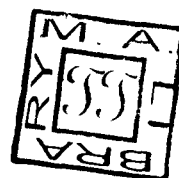
THESIS SUBMITTED FOR THE DEGREE OF  
**Doctor of Philosophy**  
IN  
BOTANY

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To the living memories of my beloved father,  
late Sh. H. Bundu, whose earnest desire  
was to see me well educated

and

To my elder brother, Dr. A.R. Wasif, without  
whose unstinting patience and cooperation  
I could not have initiated and completed  
this study.

## CERTIFICATE

Certified that the thesis entitled "Studies on the structure and activity of vascular cambium in Acacia nilotica var. telia and Prosopis spicigera" embodies a genuine research work carried out under my supervision by Mr. Muhammad Iqbal. No part of this work has ever been submitted for the award of any other diploma or degree.



( A.K.M. GHOUSE )  
Reader in Botany.





### A B S T R A C T

Anatomical studies on the structure and activity of vascular cambium in the stem of Acacia nilotica var. talia and Prosopis spicijera were carried out for three consecutive calendar years (1975-1977) with an aim to understand the behaviour of the cambium, the formation of its derivative tissues and their variations in relation to season and to the age of the tree.

The results obtained indicate that the vascular cambium, non-stratified in both the species, develops first in the fasciular region and then extends to the inter-fasciular one to form a complete ring. Once established, it necessarily contains the usual two types of cells, namely, fusiform initials and ray initials, the former being vertically aligned in tiers while the latter usually grouped into fusiform bodies - the ray initial units of different dimensions. The fusiform initials, mostly multinucleate in Acacia and uninucleate in Prosopis, vary in length in relation to seasonal variations as well as to tree age. Their mean length increases with increasing girth of the stem axis, but declines slightly after having reached certain maximum. The overall increase does not exceed 75% and 40% of their initial length recorded in the first year shoots of Acacia and Prosopis respectively.

Mean length of fusiform initials in adult tree trunks undergoes variation with respect to season also. In Mangia, the cells are comparatively shorter in April and further in August-September. Their relative proportion tends to be greater during the grand growth period. In Prosonis, the length of the initials increases from February till June, suffers a decline further till September, and then again increases during winter. Their proportion exhibits no regular variation trend.

On the other hand, ray initials, homogenous in both the species, undergo greater multiplication in order to increase their number as the trunk grows older and wider. New ray initials arise either from an apically cut cell at the end of fusiform initials, or from a lateral cell cut off the side and occasionally by transverse segmentation of a whole or a part of the fusiform initial.

Relative abundance of the ray initial units of diverse width and height also varies with the growing girth of the stem axis, the percentage of broader units going high in older trunks. Similarly, the ray initials occupy relatively more of the tangential area of cambial zone in older trunks. However, even in younger shoots, their relative proportion does not drop as much as to remain only 10% or less than that, and thus, counter to the generalisations derived from

observations of some earlier workers working with temperate species.

The bark, divisible into zones of conducting phloem, non-conducting phloem and rhytidome, increases in thickness with the growing axis girth but the bark-wood ratio which is 1 : 2 and 1 : 3 in young axes of Acacia and Prosopis, becomes 1 : 11 and 1 : 16 in their main trunks respectively. Of the phloem elements, sieve-tube members possess compound sieve plates on their obviously inclined or oblique end walls in both the species. They usually experience monopolar intrusive growth. The sieve-tube members constitute about  $\frac{2}{5}$  to  $\frac{2}{3}$  and  $\frac{1}{5}$  to  $\frac{2}{3}$  of the conducting phloem along the stem axis of Acacia and Prosopis respectively, occupying more area in younger than in older stems.

Mean length of the sieve-tube members increases continuously with regard to the girth or, in other words, to the age of the stem axis. However, in case of Prosopis, it becomes more or less constant after attaining certain maximum in the old trunk. Their mean width also varies more or less correspondingly. The size variation is not very gradual and systematic in relation to season, although in Acacia, the length appears to remain somewhat suppressed during early months of a calendar year.

Phloem fibres, mostly septate in Acacia and aseptate in Prosopis, are distributed throughout the secondary phloem

in characteristic patterns. They grow intrusively at both ends attaining a length about 3.6 times that of mother cambial initials. The fibres may not differentiate in the conducting phloem of young shoots. When differentiated, their relative proportion decreases in Acacia and increases in Prosonia with the growing axis girth. From the top of the tree basewards, their mean length initially increases with the axis girth in both the species. However, after attaining certain maximum, it begins to decrease with further growth of the axis. As to the seasonal variation, the length tends to decline during June to September, as compared with the rest of the year. The variation pattern is, however, not very consistent.

In both the species, the amount of axial parenchyma is more in younger than in older axis. With the phloem rays, however, the reverse is to be the case.

On the inner side, the relative proportion of vessels in the sap wood of Acacia follows no systematic variation trends with varying axis girth. It, however, begins increasing with the stem girth later becoming constant in the old trunk in case of Prosonia. With respect to season, the proportion tends to be appreciably high during late summer (July-October) in Acacia, while in Prosonia, it is so during early summer (March-May).

Mean length of the vessel segments increases with certain fluctuations with the increasing axis girth, until it attains

the maximal value. With further growth of the axis, the length becomes more or less constant in Acacia, and suffers an ultimate decline in Prosopis. It remains somewhat retarded during winter (October-March) and tends to increase during summer (April-September) in case of Acacia. Conversely, it is usually greater during winter and early spring (December-April) in case of Prosopis. Mean width of the segments in both the species usually undergoes irregular changes in relation to season as well as to tree age.

Contrary to the vessel segments, xylem fibres in Acacia occupy relatively less amount of the transectional area of sap wood during late summer. In Prosopis, it is so during early summer. The fibre proportion declines almost regularly with increasing axis girth in Acacia while it increases gradually in Prosopis. Mean length of the fibres gradually increases in upper parts of the stem axis and later becomes somewhat irregular in the trunk region of Acacia. In Prosopis, on the other hand, the initial increase undergoes slight fluctuations and ultimately the length attains a constancy in basal part of the trunk. The length, however, does not exhibit any cognizable and consistent trend of variation in relation to season.

As to the activity of cambium, it initiates at different times in the two species in question. Swelling of the cambial cells occurs around mid February and mid March in the trunks

of Acacia and Prosopis respectively. It is followed by cell division within a period of 2-4 weeks. The division stops by the end of December in Acacia and late in October in Prosopis. Xylem differentiation in the two species, however, continues till January and till early November respectively. Thus, the cambium remains active for about 9½ months in Acacia and for about 7 months in Prosopis. Production of phloem precedes that of xylem in both the species.

A moderately high temperature seems to be inductive for cambial reactivation. Combined with high humidity, it enhances cell division in the cambial zone. Once initiated, the cambial activity appears to be capable of continuing even at relatively lower temperature. Emergence of new leaves precedes the cambial reactivation in both the species. A considerable gap between the new leaf formation and the cambial activity observed in Prosopis is supposed to be owing to the probable consumption of the initial amounts of auxin produced by young leaves in the flowering phenomenon which immediately follows the leaf emergence in this species.

## ACKNOWLEDGEMENTS

I bow in gratitude to the almighty Allah that by His grace and benevolence I could bring this work to an end.

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Aligarh

MUHAMMAD IQBAL

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## **I N T R O D U C T I O N**

## SCOPE OF WORK

In most dicotyledons and gymnosperms, stems continue to grow in thickness even after they have ceased to elongate and, therefore, the older the stem is, the thicker it becomes. Additional tissues that add to the girth of plant axis are usually the secondary phloem and xylem. These tissues originate from a lateral meristem which develops from pro-vascular elements between the phloem and xylem of primary vascular system and encircles the central core. This meristem is termed "vascular cambium" or simply the "cambium". In a three dimensional view, the cambium is a continuous sheath about the xylem of stems, roots and their branches, and extends in the form of strips into leaves if the latter exhibit secondary growth. In most of the plants, the cambium is reported to undergo successive active and dormant phases during a growth year, with a few exceptions among tropical species in which the meristematic activity of the cambium continues all the year round.

Behaviour of the cambium is regulated by several internal and external factors which include the heredity constitution, physiological phenomena and environmental conditions of the habitat. It is, thus, interesting to investigate the influence of different physical and climatic factors on cambial construction and activity and then to suggest measures for

the maintenance of a desirable growth pattern to ensure a vigorous production of the derivative tissues along with their useful contents like gums, oils, resins and tannins.

Although there exists extensive literature on the cambium of temperate species, the meristem is yet to be properly studied in tropical ones, especially those of India. A major contribution in this direction has come from laboratories at Aligarh and Delhi (cf. Ghouse & Iqbal 1979a). No information on the cambium of Indian acacias and mesquites is so far available, although they are of utmost importance to various industries like those of medicine, tannin, timber and textile, as well as to arid regions where they are being extensively utilized not only for reclamation of soil but also for combating with desertification and wind action. It was, therefore, considered desirable to undertake a thorough study on the structure and behaviour of cambium of these trees under varying conditions of age and season. Since this type of work involves intensive collection of materials for all the species under study, the work was confined to the following species commonly grown in and around Aligarh:

1. Acacia nilotica (L.) Willd.
2. Prosopis spicigera L.

The study mainly covers the following aspects of radial growth:

1. Formation and structure of cambium
2. Structural variation of cambium and its derivative tissues in relation to age of the tree and to seasonal changes
3. Periodicity of cambium and its relationship with phenological conditions
4. Production of secondary tissues
5. Relationship between extension and radial growths.

## CONCEPT OF CAMBIUM

A number of conflicting views are held on the nature of cambium. The cambial zone normally consists of an unbroken cylinder of meristematic cells, the fusiform and ray initials, arranged in radial files. These files extend into the mature secondary tissues where they may become obscured by changes that occur with differentiation. Dividing cells close to the mature phloem form the phloem mother cells while those contiguous to xylem are the xylem mother cells. The transition in cell type and activity through the cambial zone is gradual, particularly in the active cambium of dicotyledons, and in practice it is difficult to define the radial extent of the true cambium.

The concept of a multiseriate cambium may or may not include reference to a single permanent initial within each radial file of cells. One school of thought postulates a multiseriate zone in which all the cells are equally endowed with the multiplication capacity. This view, proposed by Raatz (1892) has been strongly supported by Cateson (1964). The other one and, of course, the most axiomatic interpretation of the cambium pleads for the existence of a single initial cell in each radial file of cambial cells which ultimately makes for the origination of all the cambial

derivatives. Such an initial lies somewhere between the phloem and xylem mother cells. This view mainly put forth by Bannan (1955, 1968a) and Newman (1956) has been convincingly substantiated by the ultrastructural studies of Mahmood (1968) and Murmanis (1970) pertaining to the tangential wall characteristics. Despite the difficulty in distinguishing the actual initials in the actively dividing cambial zone, a group of workers restricts the use of the term cambium to the initials only. Such an interpretation often used in American literature (Wilson et al. 1966; Zimmermann & Brown 1971), defines the cambium to be a functionally uniseriate layer between actively dividing xylem and phloem cells. In the present study the cambium has been considered, after Butterfield (1975), as a "multiseriate zone of periclinally dividing cells lying between the differentiating phloem and xylem with a distinct initial capable of both periclinal and anticlinal divisions lying somewhere within each radial file of cells". The proposed concept of the cambium and its derivatives is illustrated in Table 1.

TABLE 1.

Concept of vascular cambium and the terminology used for describing the associated tissues.

Name of the tissue	Characteristics
SECONDARY PHLOEM	Mature tissue
DIFFERENTIATING PHLOEM	Limited cell division, cell enlargement and secondary wall deposition
PHLOEM MOTHER CELLS	Periclinal division
CAMBIAL INITIAL	Periclinal and anticlinal division
XYLEM MOTHER CELLS	Periclinal division
DIFFERENTIATING XYLEM	Limited cell division, cell enlargement and secondary wall deposition
SECONDARY XYLEM	Mature tissue

**M A T E R I A L S**

**A N D**

**M E T H O D S**



## SELECTION OF MATERIALS

The following arid zone species of two allied genera of Mimosaceae were selected for the study:

1. Acacia nilotica (L) Willd. variety tolia.

A medium to large size ever green tree with deeply fissured, thick and blackish bark, spreading crown, feathery foliage, small spines, yellow flowers in globose heads, and constricted pods. Indigenous in India and Ceylon, this variety is typical of the species. The tree is valuable for afforestation and reclamation of waste land, finds use in tannin industry, and serves as a host for lac insects. The gum exuded from the bark is used as a sizing material in paper and textile industries as well as in dyeing and calico printing. The timber is best suited for agricultural implements, railway keys and the cart and boat building ( Hao & Purkayastha 1972, pp. 17-37 ).

2. Prosopis spicigera L.

A small to medium size tree with slender branches armed with conical thorns. The bark is greyish or dirty ash coloured, with longitudinal fissures and transverse cracks. Bearing yellow flowers in spikes, the tree is a native of Indian sub-continent. Bark of this species is used as a remedy for rheumatism and scorpion sting. The wood is used for house

building, in making agricultural implements and as a firewood ( Rao & Purkayastha 1972, pp. 54-57).

The main phenological features of both the selected species are presented in Table 2.

## PROCEDURE AND TECHNIQUES

In order to study the cambium and its immediate derivatives about a dozen fully grown, normal trees of comparable age and vigour ( Table 3 ) were selected for each species and labelled. Trees growing under shade or in poor soil conditions were avoided as they were likely to have a relatively slackened growth or other physiological abnormalities.

Collection: Blocks of about 2 cm<sup>2</sup> size containing sapwood, cambium and bark were collected from main trunks of the selected trees at chest height ( about 1.5 m from the ground ) with the help of chisel and hammer. The collections were made at fortnightly intervals, usually in morning hours, and the blocks were taken from all the four sides ( east, west, north and south ) of the trunks of at least two trees per species on each turn. This practice was extended for three consecutive years viz., 1975, 1976 and 1977. When the material was collected from the same tree repeatedly, care was taken to obtain the blocks from a place in the trunk about 20 cm apart from the previous sampling spot. To study the ontogenetic changes in the structure of cambium and its derivative tissues, samples were collected in July and November, 1976, from

different spots of the main tree axes with diverse girth and height ( Fig. 1 ). The following circumferences (C) of the stem axis were selected for this purpose:

2 cm	...	(C <sub>1</sub> )
5 cm	...	(C <sub>2</sub> )
10 cm	...	(C <sub>3</sub> )
45 cm	...	(C <sub>4</sub> )
65 cm	...	(C <sub>5</sub> )
80 cm	...	(C <sub>6</sub> )
125 cm	...	(C <sub>7</sub> )
175 cm	...	(C <sub>8</sub> )

**Fixation:** The samples were fixed on the spot in either FAA or Crafts III solution and were later aspirated for free access of the fixative into deeply situated tissues. They were allowed to remain in the fixative for 3-5 days and then transferred to a mixture of 50% ethanol and 50% glycerol ( V : V ) for softening. After a month the material was either used for sectioning or preserved in 70% ethanol.

**Sectioning and Staining:** Sectioning of the material for transverse and longitudinal ( radial as well as tangential ) sections was made on a Reicherts sliding microtome usually at a thickness of 10-12/um. Depending on the purpose of the study, the sections were stained with any of the following

staining schedules and passed through ethanol series for dehydration:

A. For the study of cambium:

- 1) Heidenhains hematoxylin ( Johansen, 1940 ).
- 11) Tannic acid-ferric chloride ( Foster, 1934 ).

B. For the study of derivative tissues:

- 1) Heidenhains hematoxylin - Safranin/Bismark brown ( Johansen, 1940 ).
- 11) Tannic acid-ferric chloride - lacmoid ( Cheadle et al., 1953 ).

Maceration: The cambium derived elements viz., vessel segments, xylem fibres, sieve-tube members and phloem fibres were macerated, when necessary, following the method described by Ghouse et al. (1974). For phloem elements, the method included slicing of the bark samples in tangential plane at approximately 1 mm thickness ( Fig. 2 ). The slices were separately treated with 5% NaOH solution at 45-50°C for a number of days. The solution was replaced with a fresh one of the same concentration after each 72 hours. Under periodical checkings, the treatment was extended till the cells of the treated slices became loose enough to allow their separation on glass slides when teased with a needle or tapped gently under the cover slip. Having attained the desired stage,

the slices were washed and stained with 1-2% aqueous solution of astra blue or lacmoid (for sieve elements) as well as with that of safranin or Bismark brown (for fibres). The macerated elements were mounted in glycerol. In case of xylem, the slices obtained from different places <sup>were</sup> separately treated with concentrated  $\text{HNO}_3$  and potassium chlorate, following the method of Ghouse & Yunus (1972) with slight modifications, and were stained with safranin or Bismark brown.

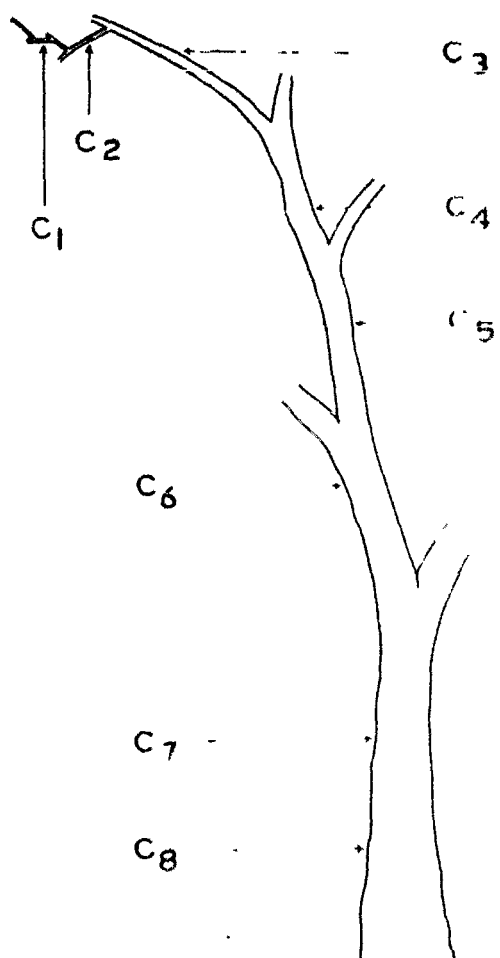
Estimation of tissue proportions: The area occupied by the component initials in cambial zone and by the different phloic and xylary elements in derivative tissues was determined by the following method.

For each sample, 10-20 camera lucida drawings of the tissue under study were made from the relevant sections on tracing papers of uniform thickness and the area occupied by the desired elements was carefully marked. All the drawings were collectively weighed in a sensitive microbalance. Of these drawings the portions containing the marked tissue elements were carefully cut and removed, and again weighed separately. Since the weight of the uniformly thick paper-sheets was directly proportional to their surface area, the area occupied by the required elements was computable by comparing the above two weights. Relative proportion of various cell types was thus calculated per unit area and

expressed in percentage following Ghouse and his co-workers (cf. Ghouse & Yunus, 1974a, b, c; Ghouse & Iqbal, 1975, 1978 ).

Dimensional measurements: To determine the size of various cell types in samples collected at a particular time or from a particular level of the tree axis, 100-250 elements per sample were usually measured on a random basis using the micrometer scale under specific magnifications. The average as well as range of the cell dimension was then determined after pooling the readings obtained from all the relevant samples taken from the four sides of tree trunk.

Besides, the ray initial units of varying heights were categorized for the sake of convenience as short (1-15 cells), medium (16-30 cells), moderately tall (31-45 cells) and extremely tall (above 45 cells). The ray units of diverse widths, on the other hand, were identified as uniseriate, biseriate, triseriate, tetraseriate and multiseriate.

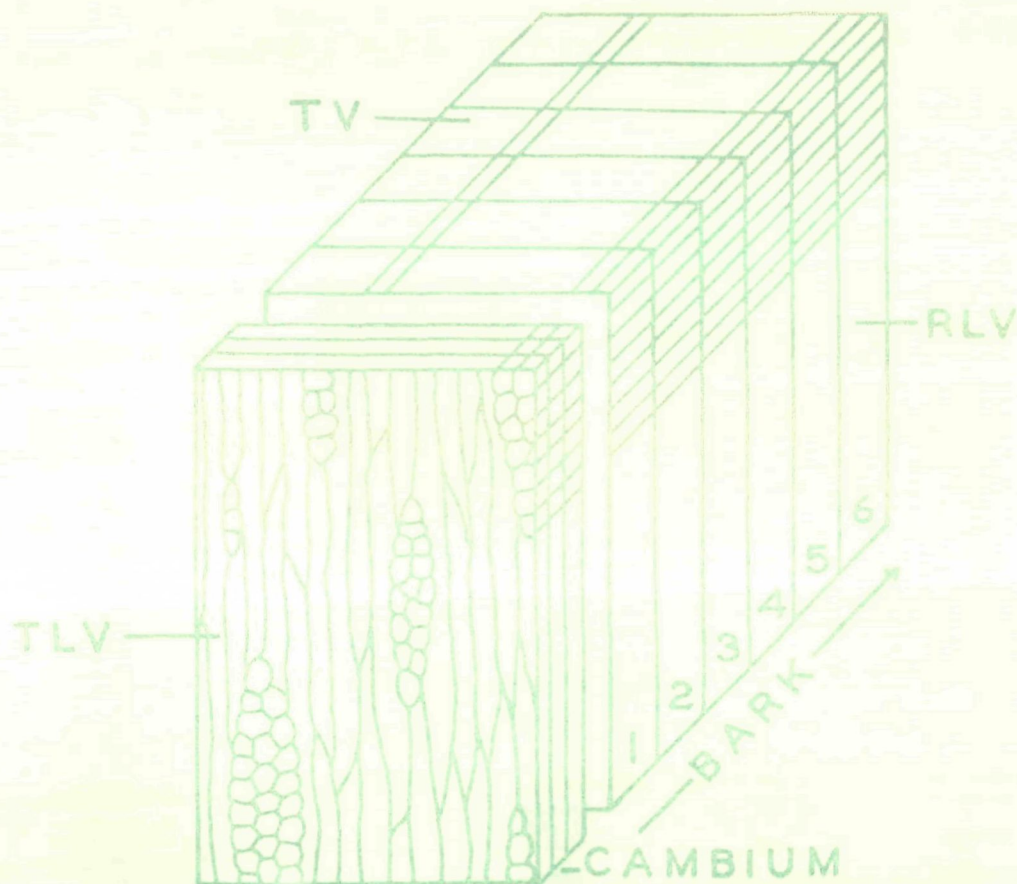


SEMIDIAGRAMMATIC SKETCH OF A TREE  
TRUNK SHOWING THE DIFFERENT  
SAMPLING SPOTS

C—CIRCUMFERENCE

11





TV—TRANSVERSE VIEW

RLV—RADIAL LONGITUDINAL VIEW

TLV—TANGENTIAL LONGITUDINAL VIEW

FIG. 2

TABLE 2

Phenological data collected during 1975-77 for the selected species growing in and around the University Campus.

Species	Leaf emergence	Flowering	Leaf fall
<u>Acacia nilotica</u> var. <u>tellia</u>	Feb.-Nov.	May-Dec.	Jan.-May
<u>Prosopis spicigera</u>	Feb.-May	March-May	Jan.-March

TABLE 3

Approximate age and size of the trees selected for the study.

Species	Age (years)	Tree height (meters)	Tree trunk circumference(cm)	Bark-wood ratio in tree trunk
<u>Acacia nilotica</u> var. <u>tellia</u> .	45-50	10-15	150-180	1 : 11
<u>Prosopis spicigera</u>	30-40	8-12	148-175	1 : 27

**O B S E R V A T I O N S**

## CLIMATE OF ALIGARH

The various growth activities of plants are now known to be greatly influenced by the environmental conditions of their habitat. It is, therefore, a must to study the local climatic factors and their variations as a prelude to a clear understanding of the growth phenomena under a particular set of epedaphic factors. The main climatic factors which have a decisive bearing on the growth activities in plants include (i) temperature, (ii) humidity and (iii) rainfall.

Analysis of the data obtained from the Meteorological Section of Physics Department, Muslim University, Aligarh, for the years 1975, 1976 and 1977 has revealed that the climatic conditions of Aligarh city which is located at 27.53°N latitude and 78.4°E longitude, are at their extremes.

Temperature: December and January are the coldest months of the year during which the mean monthly temperature usually ranges between 13°C and 17°C. The winter season, however, begins from November when the mean monthly temperature usually falls upto 18°C. May and June, on the other hand, are the hottest months with their mean temperature rising upto 34°C. Monthly average of the maximum and minimum daily temperatures is illustrated in Table 4.

Relative humidity: Monthly average of the relative humidity generally ranged from about 28 to 86% during the years of study. April and May are comparatively dry months but soon after the monsoon sets in, humidity goes up. July, August and September are the most humid months after which the humidity declines steadily. Monthly average of values recorded in the morning ( 8.30 a.m. ) and evening ( 5.30 p.m. ) hours are shown in Table 5.

Rainfall: The rainy season in Aligarh usually commences from mid-June and continues till August or September. It is in this period of the year that Aligarh receives about 90% of the total annual precipitation of about 1000 mm. The rainfall in winter is scanty and sporadic ( Table 6 ).

TABLE 4

Mean monthly temperature (in °C ) recorded at Aligarh during 1975, 1976 and 1977. Parentheses include the mean of minimum and maximum values.

Months	1975	1976	1977
January	13.4 ( 8.1 - 18.7 )	14.6 ( 8.9 - 20.4 )	14.4 ( 7.5 - 21.3 )
February	15.4 ( 9.8 - 21.1 )	16.5 (10.0 - 22.2 )	17.6 ( 9.5 - 25.8 )
March	21.1 (14.4 - 27.8 )	21.0 (14.3 - 27.8 )	24.8 (14.5 - 35.2 )
April	28.2 (21.1 - 35.3 )	27.4 (20.5 - 34.4 )	28.7 (20.7 - 36.7 )
May	32.2 (26.0 - 38.4 )	30.6 (24.2 - 37.0 )	30.3 (23.4 - 38.4 )
June	30.3 (26.3 - 34.4 )	30.6 (26.1 - 35.2 )	33.1 (26.4 - 39.8 )
July	29.0 (25.9 - 32.2 )	29.7 (26.6 - 32.9 )	28.7 (25.8 - 31.7 )
August	28.5 (25.8 - 31.1 )	27.5 (25.2 - 29.7 )	29.6 (26.0 - 33.2 )
September	28.3 (27.0 - 29.6 )	28.6 (23.8 - 33.5 )	27.9 (24.2 - 31.7 )
October	27.0 (24.2 - 29.8 )	27.4 (19.4 - 35.4 )	26.9 (20.4 - 33.5 )
November	17.9 (10.9 - 24.8 )	22.0 (14.3 - 29.5 )	23.0 (15.7 - 30.4 )
December	14.9 ( 8.3 - 21.6 )	15.7 ( 7.9 - 23.5 )	17.3 ( 9.9 - 24.7 )

TABLE 5

Mean monthly relative humidity recorded at Aligarh during 1975, 1976 and 1977. Parentheses include the mean of readings taken in morning (8.30 a.m.) and evening (5.30 p.m.) hours respectively.

Months	1975	1976	1977
January	73.3 (79.2 - 67.4 )	68.0 (78.3 - 57.7 )	63.1 (72.5 - 53.8 )
February	59.6 (73.6 - 45.6 )	63.5 (75.2 - 51.9 )	61.2 (74.0 - 48.5 )
March	58.5 (73.8 - 43.2 )	47.3 (58.3 - 36.4 )	42.1 (53.6 - 30.6 )
April	28.2 (32.3 - 24.1 )	32.2 (41.1 - 23.3 )	42.7 (52.1 - 33.3 )
May	37.7 (50.8 - 24.5 )	40.8 (45.8 - 35.8 )	42.0 (50.0 - 34.1 )
June	56.4 (60.7 - 52.0 )	50.6 (57.8 - 43.5 )	46.2 (53.7 - 38.7 )
July	74.3 (79.4 - 69.1 )	76.8 (80.7 - 73.0 )	86.2 (88.9 - 83.5 )
August	80.2 (85.3 - 75.0 )	83.2 (86.2 - 80.3 )	78.2 (82.0 - 74.5 )
September	83.3 (88.1 - 78.4 )	67.7 (72.7 - 62.7 )	78.6 (84.0 - 73.3 )
October	62.9 (68.6 - 57.3 )	47.9 (55.1 - 40.6 )	66.8 (73.4 - 60.2 )
November	53.2 (61.2 - 45.3 )	56.5 (61.6 - 51.4 )	64.5 (71.0 - 58.0 )
December	60.2 (67.8 - 52.6 )	58.5 (65.5 - 51.5 )	69.3 (71.7 - 66.9 )

TABLE 6

Monthly rainfall (in mm ) recorded at Aligarh during 1975, 1976 and 1977.

Months	1975	1976	1977
January	24	0.6	35
February	9	12	3
March	5	5	0.4
April	-	12	34
May	14	23	51
June	93	35	49
July	248	355	428
August	147	427	336
September	286	74	167
October	68	-	81
November	-	-	-
December	-	-	56



## FORMATION AND STRUCTURE OF CAMBIUM

In both the species studied, the vascular cambium first developed between the primary phloem and xylem and then extended over to interfascicular regions to form a complete ring. The cambium was made up of two types of initials viz., fusiform and ray initials. The fusiform initials were roughly hexangular with long tapering ends which overlapped one another to an appreciable extent on account of apical intrusive growth. The ray initials, on the other hand, were relatively thin walled and nearly isodiametric in shape. They usually occurred in groups of varying magnitude, generally known as ray initial units ( Plates IA & IIA ). The fusiform initials were highly vacuolated, while the ray initials were generally filled with varying amounts of starch and tanniferous substances. The radial walls of fusiform initials bore primary pit fields, through which they communicated with contiguous elements by means of profound plasmodesmata. The radial walls of these elements were comparatively thicker than the tangential ones and appeared beaded, especially during the dormant phase ( Plate VI ).

A large number of fusiform initials contained more than one nuclei. In acacia, sometimes the nuclear number per cell went as high as eight, though the majority of cells had

1-5 nuclei. In multinucleate initials, the nuclei took various shapes such as spherical, elliptical and fusiform ( Plates IIIB & D, VIA & B ). Their shape varied not only in different elements but also within a cell. A few nuclei in a cell showed the signs of degeneration, after assuming an abnormal shape. In the degenerating nuclei, the nuclear content appeared to degenerate first and then the nuclear membrane. In some cases, however, the spherical nucleus first elongated to become a fusiform body with filiform ends and later underwent a complete necrosis, usually beginning from the tailed ends. The nuclei seemed to be relatively smaller and densely stained during the dormant period than in the active one.

The cambial initials underwent periclinal as well as anticlinal divisions. The former gave rise to the inner and outer derivatives and the latter multiplied their own number to enable the cambial cylinder to cope with the expanding tree trunk. In anticlinal division, a pseudotransverse wall was laid down which in the dividing elements appeared at various degrees of inclination. After such a division the daughter cells which were generally unequal in size, underwent apical elongation. As a sequel to this, the two sister cells came to lie lateral to each other. Depending on the extent of apical elongation, the fusiform initials possessed longer

or shorter tapering ends. The fully grown fusiform initials measured about 386/ $\mu$ m in Acacia and 316/ $\mu$ m in Prosopis. During a growth year, mean monthly length of fusiform initials varied from 294 to 385/ $\mu$ m in Acacia and from 263 to 314/ $\mu$ m in Prosopis. Mean monthly diameter of the ray initials varied from 12 to 18/ $\mu$ m and from 13 to 16/ $\mu$ m in the two species respectively ( Table 7 ).

Before the fusiform initials underwent pseudo-transverse divisions, their tapering ends measured in average about 63/ $\mu$ m in Acacia and 64/ $\mu$ m in Prosopis. After the division the newly formed ends of the daughter initials measured about 24/ $\mu$ m in Acacia and 18/ $\mu$ m in Prosopis. The two daughter cells, thus, had to grow 1.6 to 2.4 times over their initial length to acquire the size of the mother initial ( Table 8 ). The increase in length of the newly formed initials was accomplished mainly by apical intrusive growth which was frequently evidenced by the presence of diverse apical manifestations such as forking or bending ( Plate IVE & F ). At times, the intrusively growing fusiform cells also intruded the ray initial units usually dividing them into smaller entities ( Plate VA-C ).

As a sequel to periclinal divisions, fusiform initials generally gave rise to vertically aligned derivatives such as sieve-tube elements, vessel segments, fibres and axial parenchyma. Ray initials, on the other hand, produced radially oriented vascular rays.

The new ray initials were derived from the existing fusiform initials through transverse segmentation or by cutting off apical or lateral segments of the fusiform cells ( Plate III A-F ). At times, two or more ray initial units were found fusing together to form tall and multiseriate composite bodies ( Plate IV B & D ). Then, ray initial units of varying size came in shape through multiplication of the existing ray initials and/or conversion of the adjacent fusiform initial into ray initials ( Plate IV A & C ). This was usually brought about by the conversion of the intervening fusiform initial into a group of ray initials which formed the bridging connection between the two already existing groups of ray initials. Concurrently, splitting of tall ray initial units into smaller ones was also observed. It was owing to the intrusion of elongating fusiform initials into the ray initial units or to the conversion of any ray initial into a fusiform initial through elongation ( Plate V A-D ).

Although the over all composition of the cambial cylinder was almost the same in both the species studied, the number, size and relative proportion of the two types of initials were subject to marked variation with respect to seasonal conditions and age of the tree.

TABLE 7

Comparative size of cambial initials in adult tree trunks of the species under study. The average is based on the cell size measurement obtained throughout the year. Values in parentheses indicate the minimum and maximum monthly average in a year.

Species	Fusiform initials ( $\mu$ m)		Ray initials ( $\mu$ m)	
	Length	Width	anti-clinal diameter	Peri-clinal diameter
<u>Acacia nilotica</u>	336.2 (294-385)	16.8 (15-18)	14.1 (12-15)	15.1 (14-18)
<u>Prosopis spicigera</u>	293.1 (263-314)	16.9 (16-19)	14.9 (13-16)	13.8 (13-16)

TABLE 8

Extent of apical elongation in fusiform cambial initials of the selected species.

Species.	Average length of fusiform initials before anticlinal division ( $\mu$ m)			Average length of daughter initials ( $\mu$ m)			Growth in times
	Total length	Main body	Tapering ends	Total length	Main body	Tapering ends	
<u>Acacia nilotica</u>	386	260	63 + 63	161 + 236	74 + 149	24 + 63	1.6 to 2.4
<u>Prosopis spicihora</u>	316	187	64 + 64	135 + 203	53 + 121	18 + 64	1.5 to 2.3

DEVELOPMENTAL CHANGES IN CAMBIUM AND  
THEIR IMPACT ON DERIVATIVE TISSUES

Vascular cambium: After the differentiation of cambial initials out of procambial cells, the former undergo various dimensional and proportional changes as the tree ages. Such changes in the cambial cylinder which determine the over all structure of the cambium, also have an impact on the cambium-derived elements which constitute the secondary vascular tissues and make for their characteristic construction. Apart from the tree trunk, younger branches of varying age and girth ( Fig. 1 ) were selected to work out the developmental changes of cambium and their impact on derivative tissues.

In Acacia, fusiform initials were shorter in younger axes than in older ones. With increasing circumference of the cambial cylinder, there was a corresponding increase in length of fusiform initials till the initials attained their maximum size which was noted in C<sub>7</sub> sample obtained from the old trunk of about 125 cm circumference. Later, the size declined in the last sample (C<sub>8</sub>) taken from the basal portion of the trunk ( Fig. 3 ).

In this way, the average length of fusiform initials of this species varied from about 187/ $\mu$ m in younger axes to

327/ $\mu$ m in older trunks thereby exhibiting a 75% increase in length from younger to older elements. Width of the initials also appeared to follow a similar variation trend although it did not evince so pronounced a variation range, since they measured only 14.1 to 15.6/ $\mu$ m at the different levels of stem axis. The length of tapering ends of the initials also increased considerably with growing girth of the trunk and averaged about 43 to 69/ $\mu$ m in the different samples (Table 9).

Similar observations on ray initials revealed that they did not experience any significant change in their individual size but they, nonetheless, used to undergo greater multiplication in older stem resulting in an increased volume of ray initial units. In older branches and trunks, most of the ray initial units were relatively tall (upto 100 cells) and broad (upto 9 cells). Uniseriate as well as biseriate units were most abundant in the younger shoots and collectively formed more than 80% of the total population of rays per unit area. In relatively older branches, there was a dominance of tri and tetraseriate units. In still older axes, the tetra and multiseriate units were most abundant, their frequency reached as high as 75% in the trunk region (Table 11). Similarly, the abundance of short, medium



and tall ray initial units differed at different levels of stem axis. Short units were predominantly present throughout the axis, their relative abundance being greater (upto 79%) in younger shoots than in older ones. With growing girth of the axis, abundance of medium ray units continued to be at second place for a pretty long distance but in the trunk region their density became slightly less, while the tall ray units outnumbered the others, particularly the medium ones ( Table 13 ).

The cambial cylinder also had to expand by adding new component initials to cope with the growing girth of the axis. Fusiform initials underwent pseudotransverse divisions producing the daughter initials some of which repeated the phenomenon, while others fed away and still others gave rise to ray initials. On the other hand, some ray initials were eliminated while others divided repeatedly to produce new ones. As a sequel to all these developmental changes, there occurred a considerable variation in the relative proportion of the different cambial initials (Fig. 4). In young shoots, the fusiform initials occupied about 86% of the total tangential area of cambial zone while in mature trunks their proportion dropped to 70% ( Table 15 ).

In Prosonia, the vascular cambium developed as a wavy ring in the first year shoot and contained fusiform initials

measuring in length about 220/ $\mu$ m. The length increased gradually with increasing girth of the axis and hovered about 225/ $\mu$ m and 240/ $\mu$ m in the second-year and third-year shoots respectively. The increase in length continued with the growing axis girth till the former reached its maximum, a gradual but slight decrease then set in as the axis girth further increased ( Fig. 3 ). The over all increase in length of the fusiform cells, however, did not exceed 40% of the length recorded in the first-year shoot, as the average cell length varied from 220/ $\mu$ m to 308/ $\mu$ m at the various sampling spots. Width of these cells followed an almost similar variation pattern with respect to the axis girth. This was noted to range between 10 and 18/ $\mu$ m. Length of the tapering ends of fusiform initials measured about 60-63/ $\mu$ m in different positions of the axis ( Table 10 ).

Changes in size of ray initials did not exhibit any particular trend nor were they so pronounced. Nevertheless, their number increased considerably in the older axes through multiplication of the existing initials and also by the introduction of new ray initials on account of the conversion of fusiform initials into ray initials. At times, this conversion phenomenon led to the fusion of two or more vertically aligned ray initial units, thus, giving rise to

tall and sometimes to exceptionally tall units ( Fig.5 ).

The ray initials whose mean anticlinal and periclinal diameters hovered around 15 and 14  $\mu$ m respectively ( Table 7 ) did not experience much variation with the growing axis girth. They formed fusiform bodies varying from 1 to 7 cells in width and 1 to 100 cells in height in the different samples analyzed ( Tables 12 & 14 ). In the current year shoot of about 2 cm circumference some three-fourths of the total number of ray initial units were uniseriate. As the axis girth increased, the number of uniseriate units gradually decreased. Table 12 indicates that the width of ray initial units in younger axes varied from 1 to 4 cells. An excess of bi, and tri-seriate units was noticed at relatively greater circumferences, and of multiseriate units at still greater ones ( Fig. 5, also Plate X A-C ).

Height of the ray units at different levels of the axis girth was found to go upto 100 cells. The short and medium units collectively constituted about 90 to 99% of their total number in relatively younger shoots although this proportion dropped as much as to remain about 80% in older stems. The moderate and extremely tall units collectively formed a conspicuous proportion in the older axes ( Table 14 ).

All these changes occurring as an accommodation to the increasing circumference of the axis, resulted in a considerable change in the corresponding volume of the two types of initials. The fusiform initials occupied about 67 to 85% of the total tangential area of cambial zone in axes of diverse circumferences ( Table 15 ).

Splitting of multiseriate rays mainly caused by the intrusion of elongating fusiform initials into a pannel of ray initials or by the transformation of ray initials into fusiform ones, was found to be most frequent in the adult tree trunks upto a considerable height from the ground. The phenomenon was most common in the samples taken from the axis of 125 cm circumference ( Plate X B ).

On both the outer and inner sides, the differentiation of cells derived from the fusiform and ray initials, resulted in the establishment of (1) vertical and (2) radial systems in the secondary tissues. The amount and magnitude of the vertically aligned components were also a subject to marked variation with respect to age.

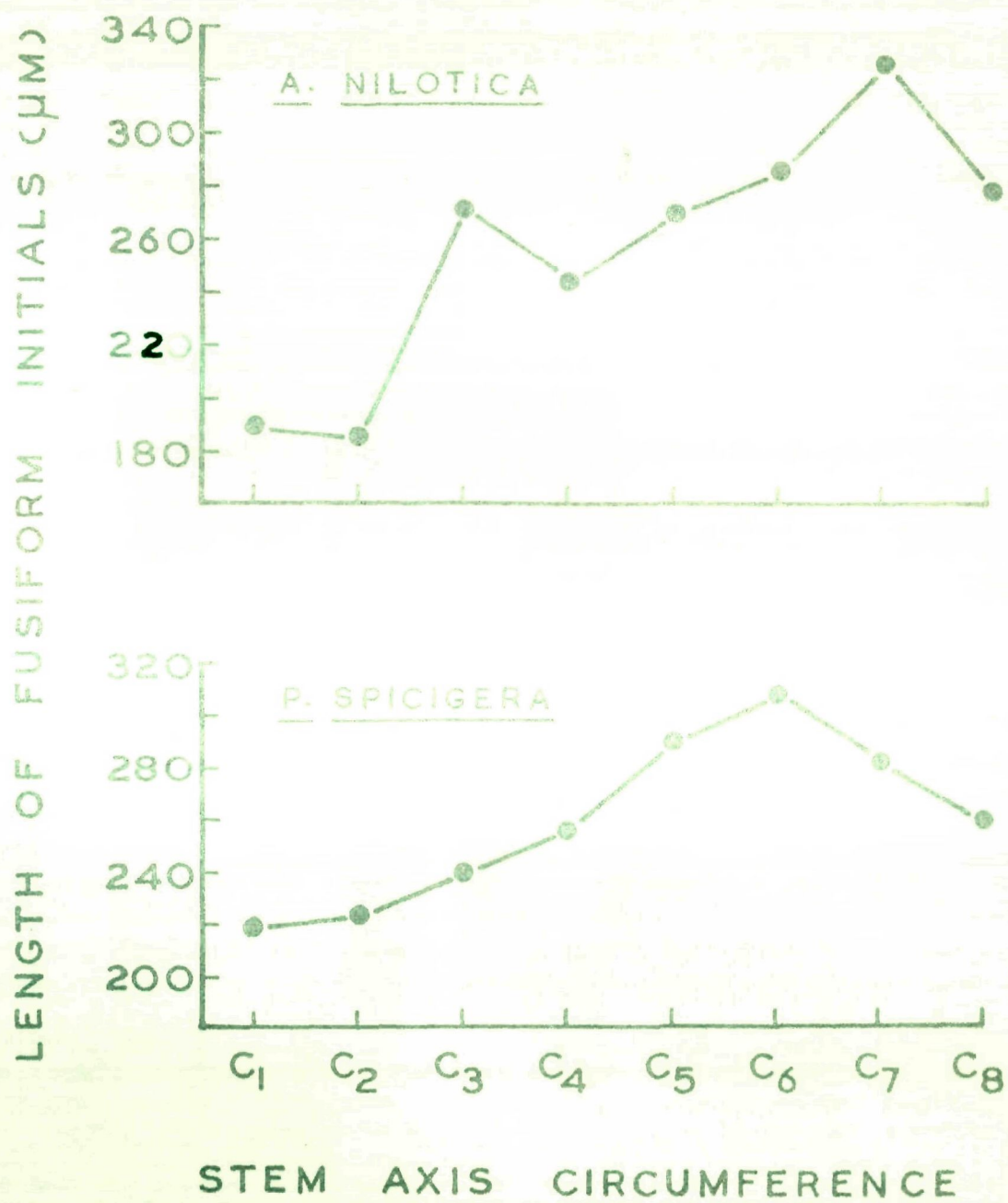


FIG. 3

TABLE 9

Size variation of fusiform initials in relation to the girth of stem axis of Acacia nilotica. The average is based on 1600-3200 independent readings. Values in parentheses indicate the range.

Stem axis circumference (cm)	Fusiform initials		
	Length (/um)	Width (/um)	Tapering ends (/um)
2	188.9 (133-266)	14.1 ( 11-19 )	43.3 ( 26-76 )
5	186.9 (114-247)	14.3 ( 9-19 )	50.9 ( 19-78 )
10	270.9 (220-323)	14.7 ( 11-19 )	63.9 ( 38-114 )
45	264.6 (197-316)	14.5 ( 9-19 )	56.1 ( 19-114 )
65	270.8 (209-380)	14.7 ( 11-19 )	61.9 ( 27-114 )
90	286.1 (190-410)	14.6 ( 11-22 )	62.6 ( 30-114 )
125	326.6 (190-381)	15.5 ( 11-21 )	68.7 ( 30-114 )
175	278.5 (209-353)	15.0 ( 11-19 )	56.2 ( 30-95 )

TABLE 10

Size variation of fusiform initials in relation to the girth of stem axis of Prosonia spicigera. The average is based on 1600-3200 independent readings. Values in parentheses indicate the range.

Stem axis circumference (cm)	Fusiform initials		
	Length (/um)	width (/um)	Tapering ends (/um)
2	220.3 (140-304)	10.5 ( 8-12 )	49.0 ( 12-120 )
6	224.5 (132-280)	13.0 ( 8-18 )	50.5 ( 12-128 )
10	239.4 (176-312)	14.2 ( 12-18 )	49.9 ( 20-112 )
45	256.9 (224-352)	16.3 ( 12-24 )	48.5 ( 20-152 )
65	289.7 (200-400)	17.6 ( 14-22 )	58.4 ( 16-156 )
90	308.5 (248-380)	17.9 ( 14-24 )	62.0 ( 12-152 )
125	281.5 (240-340)	17.2 ( 12-24 )	45.5 ( 26-120 )
175	260.6 (208-320)	16.3 ( 10-20 )	42.5 ( 20-80 )

TABLE 11

Abundance of ray initial units of varying width in relation to the girth of stem axis of Acacia nilotica. The average is based on readings from 640 microscopic fields. Range in parentheses.

Circum- ference of stem axis (cm)	Maximum width (No. of cells)	Uni- seriate (%)	Bi- seriate (%)	Tri- seriate (%)	Tetra- seriate (%)	Multi- seriate (%)
2	4	46 (43-48)	41 (38-48)	12 (10-14)	01 ( 0- 2)	-
5	4	40 (37-42)	40.5 (37-44)	19 (17-20)	1.5 ( 0- 2)	-
10	5	12 (10-14)	23 (20-24)	37 (35-40)	26 (21- 8)	02 ( 1- 4)
45	6	13 (10-14)	13 (12-15)	19 (16-21)	31 (28-34)	24 (20-26)
65	6	7 ( 4- 8)	8 ( 5-10)	19 (17-21)	30 (28-31)	36 (34-40)
90	7	8 ( 5-10)	10 ( 8-12)	10 ( 8-13)	31 (20-32)	41 (36-43)
125	9	10 ( 7-12)	9 ( 8-12)	8 ( 5- 9)	10 ( 8-12)	63 (60-65)
175	8	8 ( 5- 9)	13 (12-15)	16 (13-18)	23 (21-26)	40 (38-43)



TABLE 12

Abundance of ray initial units of varying width in relation to the girth of stem axis of Prosopis spicigera. The average is based on readings from 640 microscopic fields. Range in parentheses.

Circum- ference of stem axis (cm)	Maximum width (No. of cells)	Uni- seriate (%)	Bi- seriate (%)	Tri- seriate (%)	Tetra- seriate (%)	Multi- seriate (%)
2	3	72.5 (70-76)	27 (25-30)	0.5 ( 0- 2)	-	-
5	4	52 (50-55)	33 (30-35)	14.5 (10-16)	0.5 (00-1.5)	-
10	4	24 (22-25)	48 (45-51)	25 (24-27)	3 ( 1- 4 )	-
45	5	22 (20-24)	25 (22-28)	31 (30-36)	20 (17-23 )	2 ( 0- 3)
65	5	19 (15-21)	20 (19-24)	24 (20-26)	30 (27-34))	7 ( 3-10)
90	5	16 (15-21)	18 (15-20)	16 (15-20)	45 (41-48 )	5 ( 3- 9)
125	6	18 (15-20)	27 (25-30)	36 (30-38)	17 (15-21 )	12 ( 8-15)
175	7	15 (14-20)	18 (15-21)	31 (30-36)	23 (20-25 )	13 ( 8-15)

TABLE 13

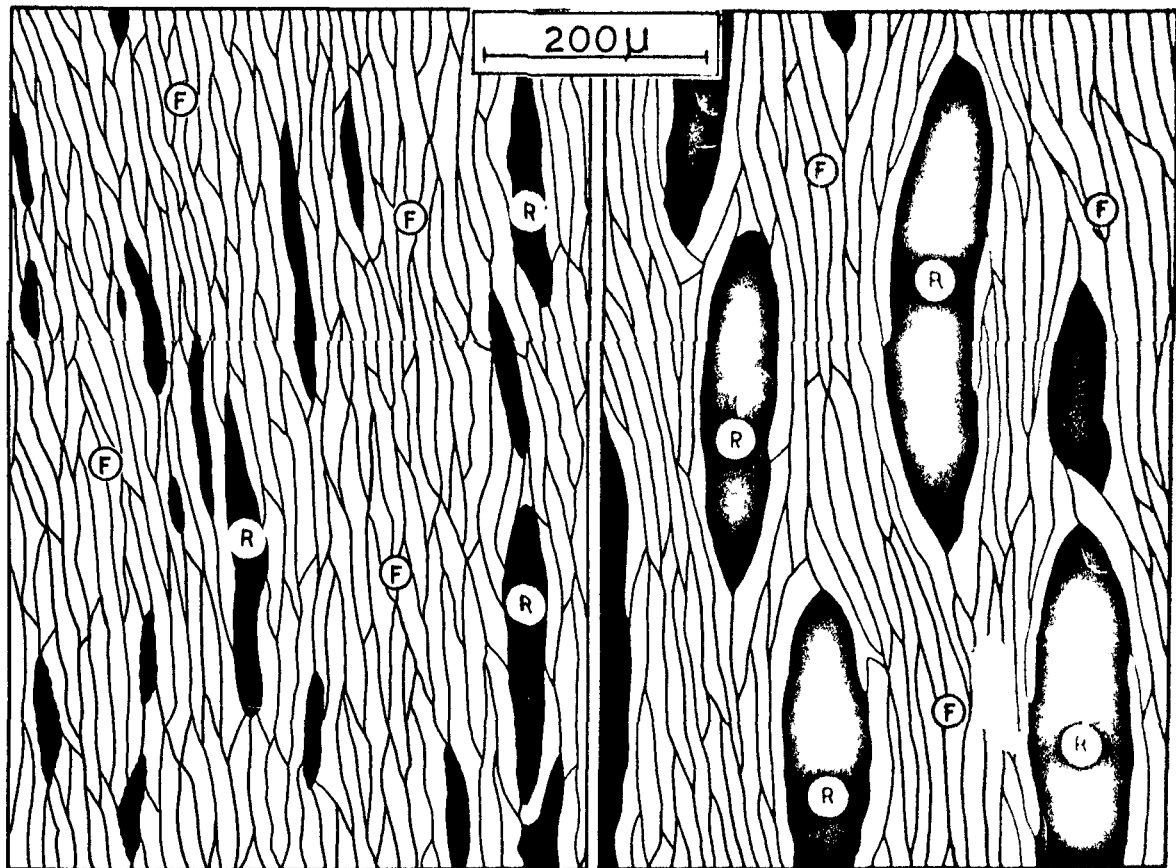
Abundance of ray initial units of varying heights in relation to the girth of stem axis of *Acacia nilotica*. The average is based on readings from 640 microscopic fields. Values in parentheses indicate the range.

Circum- ference of stem axis (cm)	Maximum height (No. of cells)	Short (1-15 cells)	Medium (16-30 cells)	Tall	
				Moderate (31-45 cells)	Extreme (above 45 cells)
2	96	79 ( 76-82 )	12 ( 9-14 )	7 ( 4- 9 )	2 ( 0- 3 )
5	82	73 ( 70-77 )	20 ( 17-22 )	6 ( 4- 9 )	1 ( 0- 2 )
10	74	45 ( 43-48 )	40 ( 37-45 )	13 (11-15 )	2 ( 1- 4 )
45	68	42 ( 40-46 )	35 ( 30-36 )	21 (18-24 )	2 ( 1- 4 )
65	95	45 ( 42-48 )	36 ( 34-40 )	15 (13-18 )	4 ( 1- 6 )
90	80	39 ( 35-41 )	30 ( 28-35 )	21 (20-24 )	10 ( 7-12 )
125	70	34 ( 30-36 )	26 ( 24-28 )	27 (23-29 )	13 ( 12-15 )
175	75	42 ( 38-45 )	28 ( 24-30 )	16 (15-21 )	12 ( 10-13 )

TABLE 14

Abundance of ray initial units of varying heights in relation to the girth of stem axis of Prosopis spicigera. The average is based on readings from 640 microscopic fields. Values in parentheses indicate the range.

Circum- ference of stem axis (cm)	Maximum height (No. of cells)	Short (1-15 cells)	Medium (16-30 cells)	Tall	
				Moderate (31-45 cells)	Extreme (above 45 cells)
2	46	86 ( 81-88 )	13 ( 10-15 )	0.9 ( 0- 2 )	0.1 ( 00-0.3 )
5	68	78 ( 73-81 )	16 ( 12-18 )	3 ( 0-4 )	1 ( 0-3 )
10	82	58.5 ( 56-60 )	37 ( 35-40 )	4 ( 3-7 )	0.5 ( 0-1 )
45	83	56 ( 52-60 )	36 ( 32-40 )	6.5 ( 2-9 )	1.5 ( 1-3 )
65	89	44 ( 42-47 )	36 ( 32-40 )	14 ( 10-15 )	6 ( 4-8 )
90	98	57 ( 50-60 )	22 ( 20-27 )	16 ( 10-18 )	5 ( 4-8 )
125	99	59 ( 55-61 )	32 ( 30-36 )	7 ( 4-10 )	2 ( 1-4 )
175	85	44 ( 41-46 )	40 ( 36-42 )	13 ( 10-15 )	3 ( 1-4 )



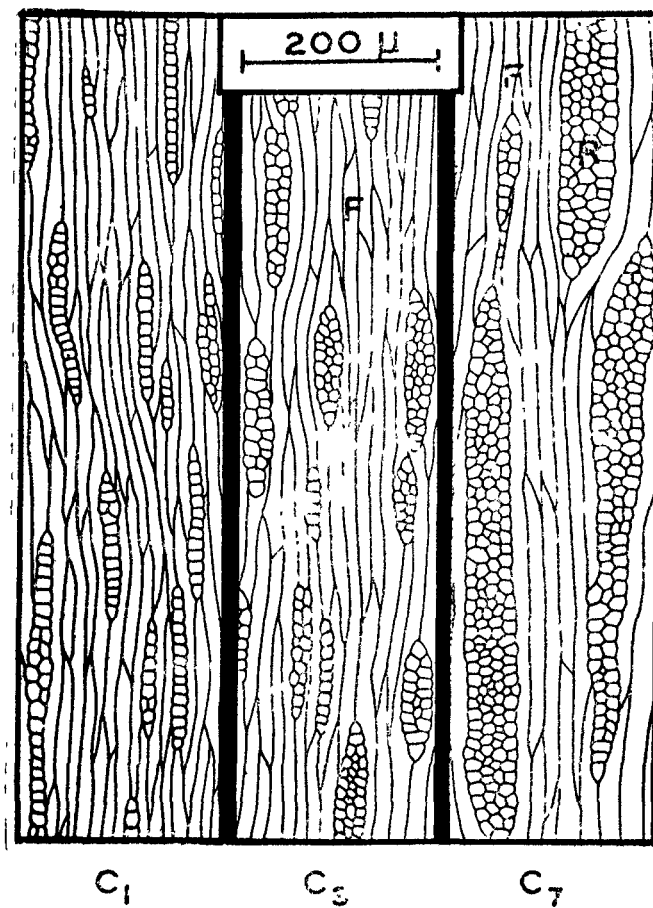
YOUNG AXIS—C<sub>2</sub>

OLD AXIS—C<sub>7</sub>

CAMBium OF A. NILOTICA IN TANGENTIAL  
LONGITUDINAL VIEW

F—FUSIFORM INITIALS  
R—RAY INITIALS

FIG. 4



CAMBium OF P. SPICIGERA IN  
TANGENTIAL LONGITUDINAL VIEW

FIG. 5

TABLE 15

Relative proportion of fusiform and ray initials in the cambium of selected species with the growing girth of their stem axes. The average is based on 320 camera lucida drawings of the cambial zone. Values in parentheses indicate the range.

Stem axis circum- ference (cm)	<u>Acacia nilotica</u>		<u>Prosopis spicigera</u>	
	Fusiform initials (%)	Ray initials (%)	Fusiform initials (%)	Ray initials (%)
2	85.6 ( 82-89 )	14.4 ( 11-18 )	81.2 ( 76-85 )	18.8 ( 15-24 )
6	86.2 ( 82-88 )	13.8 ( 12-18 )	84.8 ( 80-87 )	15.2 ( 13-20 )
10	83.8 ( 82-86 )	16.2 ( 14-18 )	83.0 ( 80-88 )	17.0 ( 12-20 )
45	78.9 ( 73-81 )	21.1 ( 19-27 )	85.0 ( 82-88 )	15.0 ( 12-18 )
65	78.0 ( 75-81 )	22.0 ( 19-25 )	77.3 ( 76-80 )	22.7 ( 20-24 )
90	76.2 ( 71-82 )	23.8 ( 18-29 )	67.2 ( 62-70 )	32.8 ( 30-38 )
125	70.7 ( 68-73 )	29.3 ( 27-32 )	76.0 ( 71-79 )	24.0 ( 21-29 )
175	71.6 ( 68-75 )	28.4 ( 25-32 )	81.0 ( 77-85 )	19.0 ( 15-23 )

Secondary phloem: In both the species studied, the annual accumulation of cambium-derived cells on the xylem side was considerably huge as compared with that on the phloem side. Further, the periodic rhytidome formation out of the non-conducting secondary phloem and then the sloughing of the outer bark in the form of scales helped to curtail the total amount of derivatives accumulated outer to cambium. These reasons, therefore, appeared to make for a gradual decrease in the bark-wood ratio with increasing girth of stem axis ( Fig. 6 ), although the over all thickness of the bark also increased noticeably ( Tables 16 & 17 ).

The amount of secondary phloem was found to increase initially with the increasing axis girth and later to maintain a more or less constant amount in older stems of both the species. On the basis of the presence or absence of functional sieve tube elements, the phloem was categorized into conducting and non-conducting zones. Sieve tube elements were intact and undamaged in the conducting region found in the vicinity of the cambial ring ( Plates IB-D, II B-D ). The phloem was taken to be non-conducting from the point where obliteration or crushing of sieve-tube members started, or the protoplast of companion cells began to disintegrate. The radial rays were somewhat deflected in the non-conducting

phloem region and usually underwent dilatation in areas near to periderms. The continuous process of the conversion of conducting phloem into non-conducting one was compensated by the addition of new cells from cambium to the conducting phloem so as to maintain the required amount of the conducting tissue. The conducting phloem in both the species was composed of sieve-tube members with one or more associated companion cells, axial parenchyma, rays and sclerenchyma. The sieve-tube members possessed compound sieve plates on their appreciably inclined or oblique end walls, and numerous sieve areas of diverse magnitude on lateral walls ( Plate IX ). The sclerenchyma, usually in the form of septate as well as aseptate fibres were found in groups forming tangentially elongated fascicles of varying size or conspicuous tangential bands (Fig. 8, Plates I-C, II C).

In both the species most of the fibre cells were found to undergo intrusive growth. This was obvious from their size as compared with the mother cambial initials and also from their structural and histochemical peculiarities such as apical manifestations, protoplasmic content, and stainability with some specific stains. The growing fibre tips exhibited various apical manifestations such as forking and serration of varying degree owing to their adjustment to the outlines of adjacent cells during the course of elongation ( Fig. 8 ).



Characterized with a comparatively broad lumen rich in cytoplasm, the fibre apices were hyaline and safranin-negative unlike the older portion of the same fibre elements or the apices of those cells which had stopped growing further and developed secondary walls. In both the species almost all the fibres showed apical elongation by both ends, the number of the elements with monopolar growth being negligible, if at all.

Some of the sieve tube members also showed indication to have grown intrusively. Unlike fibre cells, they did not exhibit any forking or serration but instead they developed small tail like apical protrusions or underwent elongation of sub-apical region pushing the terminal sieve plate aside. Mostly they had monopolar growth.

Structural changes of phloem were studied in stem axis of the same tree in relation to varying girth and height of the axis. The different phloem elements especially the fibres and sieve tube members were noted to undergo drastic changes not only in relative proportion but also in their individual dimensions in relation to the stem-width.

In the transectional view of Acacia stem, about 12-24% of the conducting phloem was comprised of the radially running rays, the remainder constituting the axial system of phloem

which consisted mainly of sieve-tube members, phloem fibres and axial parenchyma. Sieve-tube members constituted about 42-68% of the conducting phloem in axes of varying girth and height. They occupied more area in younger parts of the stem than in the older ones. Similar was the case with axial parenchyma which occupied about 12-20% of the conducting phloem zone in transections prepared from the different samples. On the contrary, the proportion of fibres exhibited an altogether different variation trend. The younger shoots had no phloem fibres. Their existence was first noticed in the 4th sample ( Table 18 ). From there onwards, their relative proportion was found to decrease with the increasing girth or decreasing height of the stem, except in the last sample taken from the basal part of the trunk ( Table 18 ).

As to the matter of dimensional changes, the length of sieve-tube members showed a gradual increase with increasing stem width. The variation in length was, however, well pronounced in younger axes only. In older trunks, the difference was meagre and insignificant ( Fig. 7 ). The average length of sieve-tube members in the current year shoots was about 164/ $\mu$ m while it measured upto 299/ $\mu$ m in samples obtained from the adult tree trunk. Width of the members also varied more or less corresponding to the length variation trend, although the variation here was not so obvious

and distinctly marked. The average diameter of the sieve-tube lumen measured about 15/ $\mu$ m in the younger shoots and almost double this amount in the basal portion of the trunk ( Table 20 ). Degree of inclination of the end walls bearing sieve-plates was also found varying in different positions of the stem axis. It did not evince any systematic and gradual variation trend, however. The angle of inclination averaged from 26 to 41 degrees at the various sampling spots ( Table 20 ).

Size of phloem fibres was also subject to variation at the different levels of stem axis but, unlike that of sieve-tube members, it did not go on increasing from the top of the tree toward the base. The fibre length, being minimum in the current year shoot, initially increased with the increasing axis girth, till it reached certain maximum. For further increase in the trunk width, the reverse was to be the case, i.e., the length declined as the trunk grew older and thicker. However, in the last sample obtained from near the base proper, the fibre length again shot up measuring almost equal to the maximum average length found around the mid-height of the trunk. Some similar fluctuations were noted for the width of fibres in this species ( Table 22 ).

Size of ray cells and axial parenchyma also varied a little. Ray cells measured about 42-100/ $\mu$ m for their average

length all along the stem axis, the longer elements being usually found in the older parts. Cell size variation was incongruous and rather inconspicuous in case of axial parenchyma. They, however, measured about 35-48/ $\mu$ m and 12-19/ $\mu$ m for their average length and width respectively.

In case of Prosopis, the phloem rays occupied about 10-20% of the transectional area of conducting phloem while the rest was shared by the vertically aligned elements. The rays occupied more area in older parts of the axis than in younger ones. Among the vertically oriented cells, the sieve-tube elements formed the major portion of the phloem, their relative proportion being greater in relatively younger axes than in older ones. It varied from nearly 21-66% along the axis. On the other hand, the amount of sclerenchyma, mostly fibres, was relatively greater in older parts of the trunk. No cognizable variation trend could be observed for axial parenchyma. Relative proportion of the fibres and axial parenchyma varied at the different levels of stem axis from zero to 35% and from 21 to 40% respectively ( Table 19 ).

As regards the dimensional variation of the phloem elements, the sieve-tube members were noted to increase in length gradually from the top of tree downwards and later to attain a constancy after having reached certain maximum ( Fig. 7 ). Their mean length varied from 166/ $\mu$ m in young

shoots to 305/ $\mu$ m in old trunks. The average width of the elements also followed a similar trend but with a tendency to narrow down slightly in the basal portion of trunk. It varied from about 12 to 28/ $\mu$ m along the stem axis. Average inclination of the sieve-tube end walls varied from 23 to 33 degrees. They were less inclined in younger shoots than in older ones. From the top toward the base, it varied in an almost increasing order occasionally beset with slight fluctuations ( Table 21 ).

The average length of fibre cells experienced an initial increase followed by a gradual fall in relation to the increasing girth or decreasing height levels of stem axis. It varied from about 1019 to 1200/ $\mu$ m in the axes of diverse diameters. Average fibre width, however, kept increasing slightly with some minor fluctuations as the axis grew older and thicker. It raised from about 10/ $\mu$ m in younger portions of the axis to 18/ $\mu$ m in older ones ( Table 22 ). Dimensional variation of axial parenchyma and ray cells was, however, not so profound and noticeable. Their lengths averaged to be about 30-50/ $\mu$ m and 40-86/ $\mu$ m respectively.

Variation in size of phloem fibres and sieve-tube members was also analyzed in relation to distance from cambial cylinder along the radius in adult tree trunk at a chest-height level ( 1.5 meter above the ground). The fibre cells

found in the vicinity of cambium were shorter than those near the bark periphery in both the species. To start from the cambium outwards, the fibre length experienced an initial decrease subsequently followed by an increase toward the periderms in case of Acacia ( Fig. 9 ). The average length here varied from 1083/ $\mu$ m to 1189/ $\mu$ m at varying distances from cambium along the chosen radius. In Prosopis, on the other hand, the average fibre length, ranging from 1058 to 1600/ $\mu$ m, underwent an initial increase near the cambium followed by an ultimate fall in the peripheral region (Fig. 9 ). Mean width of the fibres also varied a little, more or less following the trend of length variation in each species.

Sieve-tube members exhibited only a slight variation in size. Their mean length in different positions across the bark ranged from 298 to 331/ $\mu$ m in Acacia and from 262 to 314/ $\mu$ m in Prosopis. In both the species, the elements differentiated near the cambial cylinder were longer than those away from it. Their length declined consistently from the cambium outwards with some occasional vicissitudes ( Fig. 10 ). Mean width of the elements showed no regular variation trend in any of the species.

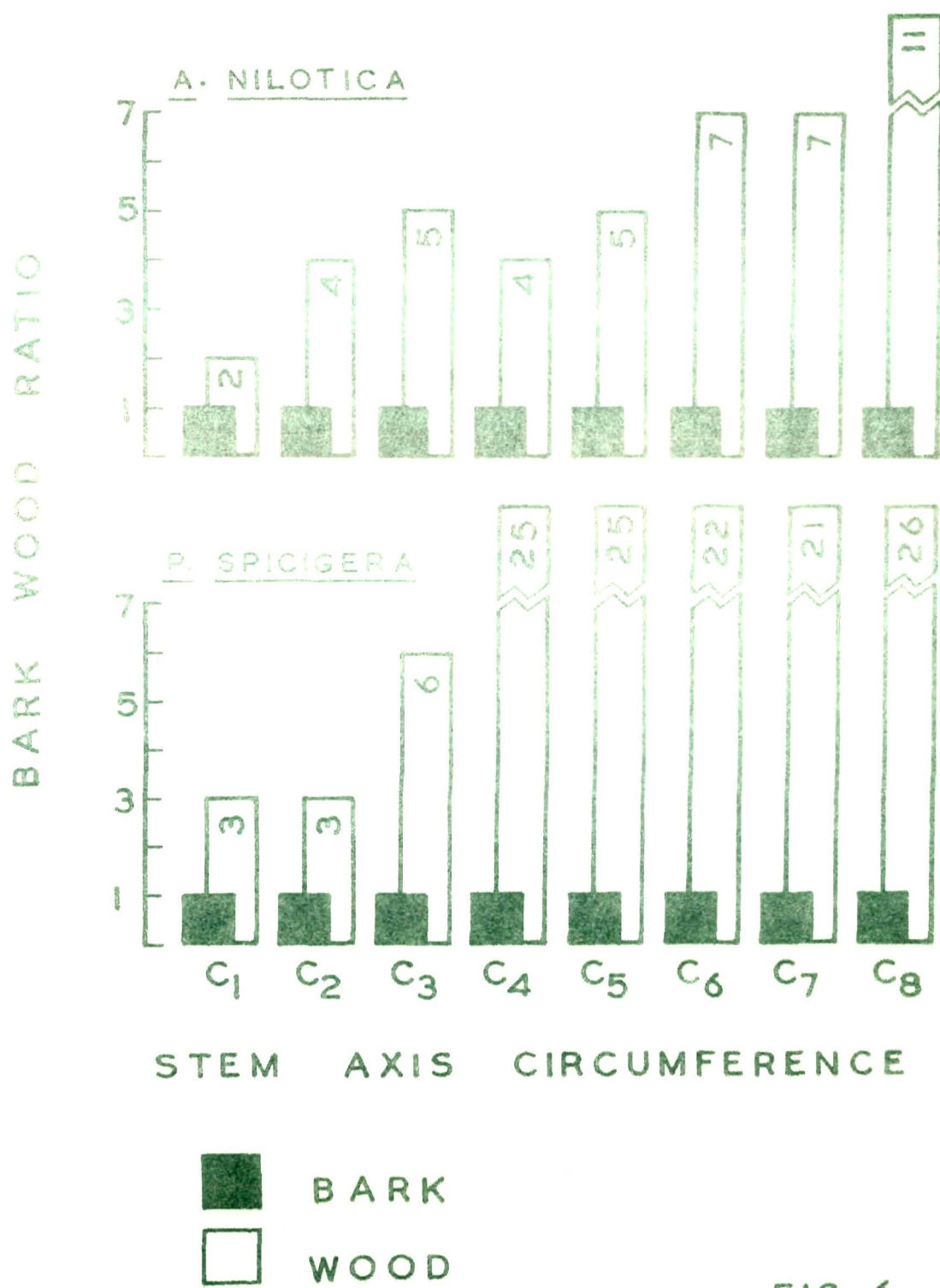


FIG. 6

TABLE 16

Thickness of bark and its component zones with respect to the girth of stem axis of Acacia nilotica.

Circum- ference of stem axis (cm)	Bark (mm)	Conducting phloem (mm)	Non-conduct- ing phloem (mm)	Rhytidome (mm)
2	1.09	0.03	0.85	0.21
5	1.59	0.14	1.27	0.18
10	2.52	0.17	1.83	0.52
45	13.13	1.13	5.75	6.25
65	18.12	1.12	8.88	8.12
90	16.81	1.66	6.11	9.04
125	24.20	3.01	7.61	13.58
175	23.22	1.67	7.27	14.28



TABLE 17

Thickness of bark and its constituent zones with respect to the girth of stem axis of Prosopis spicigera.

Circum- ference of stem axis (cm)	Bark (mm)	Conducting phloem (mm)	Non-conduct- ing phloem (mm)	Rhytidome (mm)
2	0.72	0.03	0.64	0.05
5	1.90	0.16	1.68	0.06
10	2.18	0.14	1.92	0.12
45	2.72	0.58	1.24	0.90
65	3.94	0.87	1.89	1.18
90	6.20	0.91	2.78	2.51
125	9.00	1.04	1.66	6.30
175	10.16	1.26	2.90	6.00

TABLE 18

Variation in transectional area occupied by different phloic components in conducting phloem of Acacia nilotica with the growing girth of stem axis. The average is based on 320 camera lucida drawings of the phloem. Range in parentheses.

Stem axis circumference (cm)	Sieve-tube members (%)	Phloem fibres (%)	axial parenchyma (%)	Phloem rays (%)
2	68 ( 64-70 )	-	20 ( 16-25 )	12 ( 11-14 )
5	67 ( 65-70 )	-	19 ( 16-22 )	14 ( 12-15 )
10	71 ( 65-76 )	-	16 ( 14-20 )	13 ( 11-15 )
45	50 ( 46-55 )	24 ( 19-28 )	14 ( 11-20 )	12 ( 10-12 )
65	46 ( 41-50 )	23 ( 19-27 )	14 ( 11-18 )	18 ( 15-20 )
90	42 ( 40-48 )	16 ( 12-20 )	15 ( 11-20 )	24 ( 21-25 )
125	56 ( 51-61 )	14 ( 12-20 )	12 ( 8-16 )	18 ( 15-21 )
175	51 ( 47-56 )	18 ( 15-24 )	14 ( 12-18 )	17 ( 14-18 )

TABLE 19

Variation in transectional area occupied by different phloic components in conducting phloem of Prosopis spicigera with the growing girth of stem axis. The average is based on 320 camera lucida drawings of the phloem. Range in parentheses.

Stem axis circumference (cm)	Sieve-tube members (%)	Phloem fibres (%)	Axial parenchyma (%)	Phloem rays (%)
2	47 ( 40-49 )	-	40 ( 36-45 )	13 ( 12-15 )
5	52 ( 48-59 )	0.6 ( 0- 2 )	37 ( 32-42 )	10 ( 8-13 )
10	66 ( 62-69 )	-	21 ( 17-24 )	13 ( 11-16 )
45	37 ( 33-38 )	19 ( 14-25 )	32 ( 28-38 )	12 ( 10-13 )
65	25 ( 22-29 )	28 ( 25-33 )	30 ( 27-36 )	17 ( 14-20 )
90	27 ( 25-31 )	28 ( 25-34 )	25 ( 20-29 )	20 ( 17-25 )
125	21 ( 17-25 )	35 ( 30-40 )	26 ( 20-28 )	18 ( 14-20 )
175	33 ( 30-37 )	19 ( 18-26 )	32 ( 28-39 )	16 ( 12-20 )

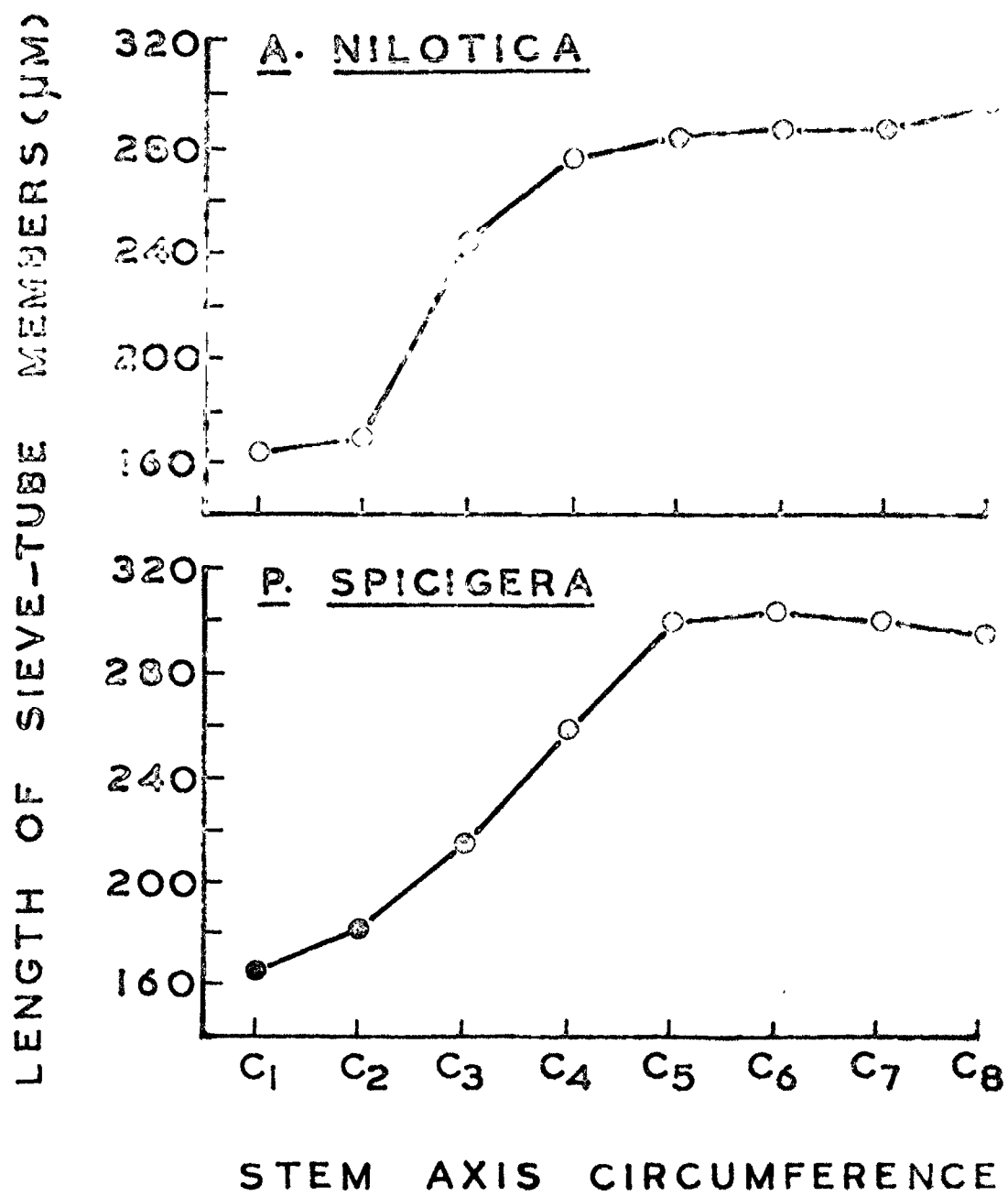


FIG. 7

TABLE 20

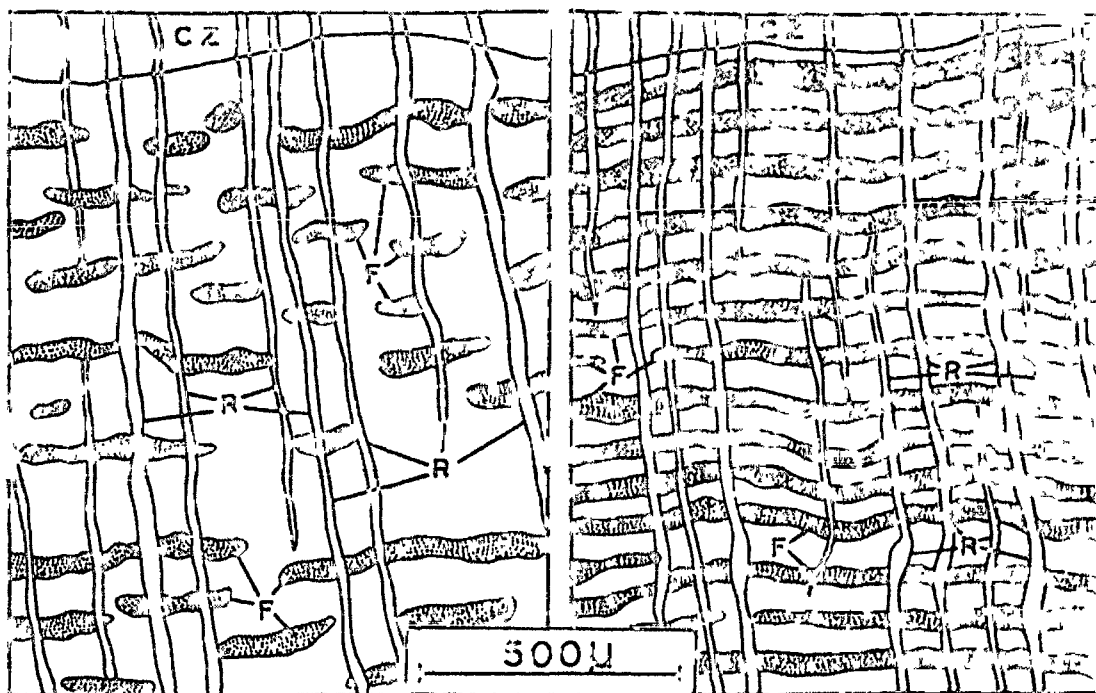
Size variation of sieve-tube members in the conducting phloem of Acacia nilotica with growing girth of stem axis. The average is based on 1600 independent readings. Values in parentheses indicate the range.

Circumference of stem axis (cm)	Length ( $\mu$ m)	width ( $\mu$ m)	End wall inclination (degrees)
2	164.3 ( 76-228 )	15.1 ( 11-19 )	25.8 ( 15-40 )
5	169.5 ( 76-228 )	15.1 ( 11-19 )	34.5 ( 15-50 )
10	243.9 ( 114-418 )	20.8 ( 15-38 )	41.0 ( 20-70 )
45	276.5 ( 190-380 )	19.8 ( 15-31 )	33.5 ( 20-60 )
65	283.9 ( 190-380 )	20.1 ( 15-31 )	35.1 ( 20-60 )
90	286.3 ( 170-390 )	20.9 ( 19-38 )	33.2 ( 15-60 )
125	288.8 ( 133-380 )	26.4 ( 19-38 )	30.7 ( 15-50 )
175	298.5 ( 170-410 )	28.5 ( 19-38 )	31.2 ( 15-60 )

TABLE 21

Size variation of sieve-tube members in the conducting phloem of Prosonia spicigera with growing girth of the stem axis. The average is based on 1600 independent readings. Values in parentheses indicate the range.

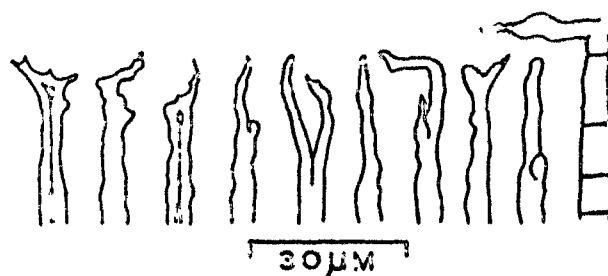
Circumference of stem axis (cm)	Length ( $\mu$ m)	Width ( $\mu$ m)	End wall inclination (degrees)
2	166.1 ( 90-210 )	12.0 ( 7.5-17 )	23.8 ( 14-35 )
5	182.2 ( 101-248 )	17.4 ( 7.5-22 )	23.1 ( 10-35 )
10	215.6 ( 120-305 )	14.6 ( 11-22 )	26.6 ( 15-42 )
45	259.1 ( 171-318 )	22.0 ( 14-30 )	25.5 ( 15-45 )
65	299.2 ( 156-367 )	26.9 ( 14-39 )	30.7 ( 16-40 )
90	304.6 ( 220-367 )	28.4 ( 15-39 )	30.3 ( 10-42 )
125	299.2 ( 171-367 )	22.9 ( 13-30 )	27.8 ( 12-50 )
175	295.8 ( 195-343 )	22.9 ( 17-39 )	33.3 ( 15-75 )



A. NILOTICA

P. SPICIGERA

PHLOEM FIBRE DISTRIBUTION



FIBRE APICES

CZ—CAMBIAL ZONE

F—FIBRES

R—RAYS

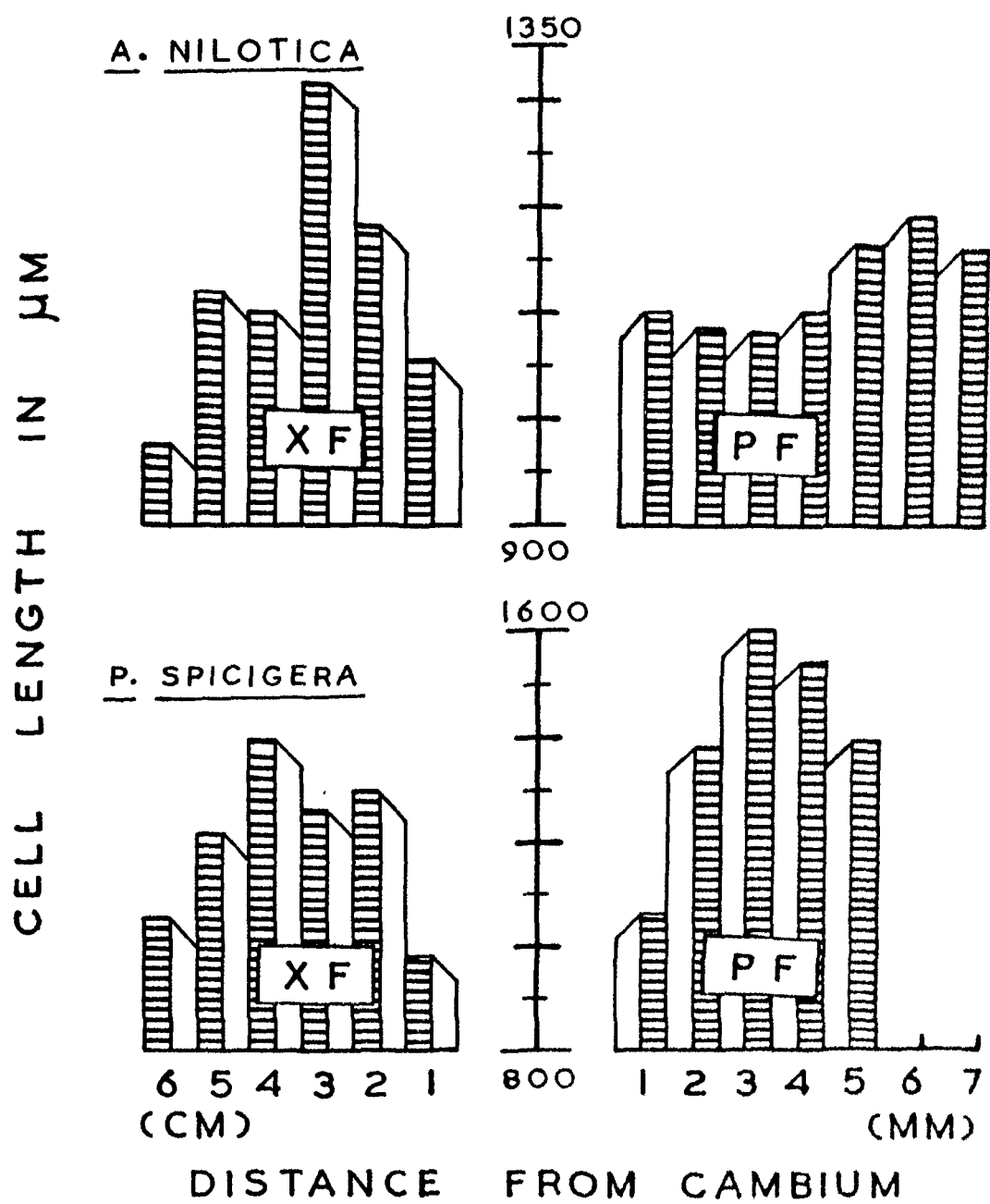
FIG. 8

TABLE 22

Size variation of phloem fibres in the secondary phloem of Acacia and Prosopis in relation to the girth of stem axis. The average is based on 4000 independent readings. Values in parentheses indicate the range.

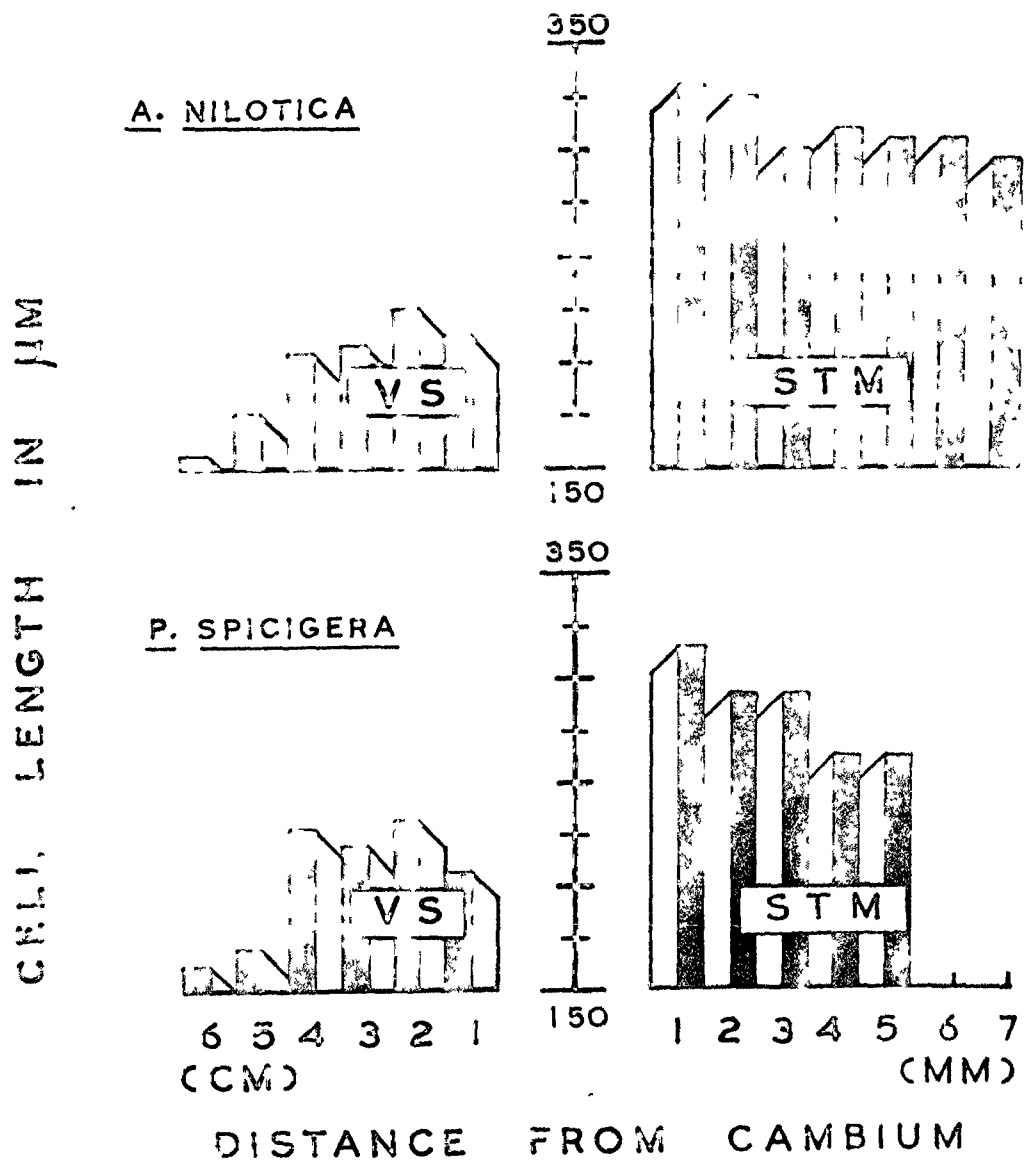
Circum- ference of stem axis(cm)	<u>Acacia nilotica</u>		<u>Prosopis spicigera</u>	
	Fibre length ( $\mu$ m)	Fibre width ( $\mu$ m)	Fibre length ( $\mu$ m)	Fibre width ( $\mu$ m)
2	986.0 ( 300-1680 )	11.4 ( 4-20 )	1019.2 ( 640-1800 )	10.2 ( 6-14 )
5	1116.8 ( 320-2450 )	14.2 ( 8-24 )	1020.6 ( 640-1880 )	10.8 ( 8-20 )
10	1188.4 ( 380-3200 )	16.0 ( 4-28 )	1139.2 ( 640-1920 )	14.4 ( 8-20 )
45	1162.2 ( 320-2560 )	16.6 ( 8-26 )	1196.0 ( 880-1860 )	16.9 ( 8-24 )
65	1098.0 ( 385-2560 )	14.9 ( 8-24 )	1096.0 ( 720-1600 )	16.6 ( 8-26 )
90	1089.8 ( 400-2450 )	14.2 ( 8-24 )	1062.0 ( 720-1440 )	18.4 ( 8-26 )
125	1081.2 ( 380-2400 )	15.6 ( 4-24 )	1058.2 ( 480-1280 )	16.2 ( 8-22 )
175	1121.8 ( 380-3200 )	16.8 ( 4-28 )	1022.0 ( 500-1376 )	18.0 ( 8-24 )





XF=XYLEM FIBRES  
PF=PHLOEM FIBRES

FIG. 9



VS=VESSEL SEGMENTS

STM=SIEVE-TUBE MEMBERS

FIG. 10

Secondary xylem: Both the species had diffuse porous wood with vessels usually isolated from each other or sometimes occurring in radial multiples of 2-3, occasionally more. Isolated vessels were almost circular or oval in transectional outlines. Besides, the wood contained paratracheal parenchyma ( i.e., parenchyma associated with vessels), and fine radial rays ( Plate X D-E ). The annual increment of cells on the wood side was much more than that on the bast side. With the increasing age of the mother meristem, the amount and structure of wood also appeared undergoing certain changes.

In the conducting part of secondary xylem, the relative proportion of radial rays in transection lay around 13-22% at the different places in Acacia stem, the remainder being formed by the axial system. Proportion of the wood rays was noted to increase gradually from the tree-apex downwards except near the base where the proportion lowered down slightly. Range of the variation was not so significant, however. Of the axially oriented elements, fibre cells formed the major component encompassing nearly 43-61% of the total transectional area in the axes of varying girth and height. The fibre proportion was observed to decline almost regularly with increasing axis girth. The last sample taken from the basal part of the trunk with maximum stem-width was, however, an exception ( Table 23 ). Axial parenchyma and vessel segments occupied about 9-16% and 14-26% respectively. From

top to the base, the amount of axial parenchyma exhibited an initial increase for some distance ( upto the 3rd sample ) but further from the fifth sample to the last one, it suffered a gradual decline. The fourth sample obtained from the axes of 45 cm circumference brought forth an abrupt drop in the parenchyma proportion, thus, disturbing the regularity of the variation pattern. Concomitantly, the variation in amount of the vessels did not show any cognisable variation trend in relation to the growing axis girth ( Table 23 ).

As the tree aged, the wood elements also experienced dimensional changes. Mean length of vessel segments usually varied from 126-211/ $\mu$ m along the axis as evident from the samples analysed. Keeping the first sample aside, the average vessel-segment length used to increase with increasing axis girth and later to attain constancy after having reached certain maximum somewhere near the mid of the stem axis ( Fig. 11 ). Surprisingly, the first sample taken from the current year shoot was found to contain the longest vessel segments. Average width of the segments underwent irregular changes. Likewise, no cognisable variation trend could be detected for the degree of inclination of their perforated end walls ( Table 25 ). Mean length of xylem fibres, increasing gradually in the upper part of the stem, became somewhat irregular in the trunk region. It varied from 925/ $\mu$ m ( in young shoots ) to 1140/ $\mu$ m ( in main trunk ).

Similar observations with Prosopis spicigera revealed that the axial system in wood of this species constituted about 82-87% of the total wood. To elaborate further, the relative proportion of vessels was noted to constitute about 10-21% in transections obtained from the axes of different circumferences. After having a gradual initial gain in the upper portion of the axis, the proportion remained almost constant all along the older stem, except in the basal part of the trunk where the amount of vessels suddenly shot up once again. Side by side, the proportion of fibres gradually increased while that of the axial parenchyma decreased in relation to the growing axis girth ( Plate X D-E ) with the exceptional deviation from the normal trend again in the last sample taken from the basal portion. The variation ranged at different places of the axis from 23-58% in case of fibres and from 15-54% in case of parenchyma. No distinct variation trend could be noticed for the proportion of radial rays. It was, however, slightly greater in adult tree trunks than in juvenile axes ( Table 24 ).

Average length of the vessel segments in Prosopis spicigera varied from 116-220/ $\mu$ m at the different sampling spots. From the top of the tree downwards, the length usually underwent an almost gradual increase till certain limit beyond

which there was an ultimate decline near the base ( Fig. 11 ). The average width of the segments gained an ultimate increase from the top towards the base, with some minor irregularities ( Plate X D & E ). It varied from 65-157/ $\mu$ m. Degree of the end wall inclination in vessel segments was a little bit higher ( upto 80 ) in younger shoots than in older trunks where it dropped upto 68 ( Table 26 ).

In case of fibres, an initial increase in length was followed by a slightly irregular deviation, ultimately attaining a constancy at the basal part of the tree trunk. The average length varied from 902 to 1045/ $\mu$ m. Similarly, the average fibre width was noted to increase for some distance from the tree apex basewards and later to get stabilized near the base ( Table 27 ). No conspicuous dimensional changes were marked for ray cells and axial parenchyma.

When analyzed in relation to distance from cambial cylinder, the mean length of fibres as well as of vessel segments was found to increase from the pith toward the cambium for a considerable distance after which the length either declined continuously or experienced somewhat irregular fluctuations near the cambium ( Figs. 9 & 10 ).

A comparison based on the annual average of length of the various types of axially oriented elements in the adult

tree trunk of both the species demonstrated that (i) sieve-tube members were to a great extent comparable in length to fusiform cambial initials, (ii) vessel segments of the sap wood were shorter than fusiform initials and sieve-tube members, and (iii) xylem fibres were either shorter than or almost equal to the contemporary phloem fibres ( Fig. 12 ).

TABLE 23

Variation in transectional area occupied by wood components in the sap wood of Acacia nilotica in relation to the growing girth of tree axis. The average is based on 320 camera lucida drawings of the wood. Range in parentheses.

Stem axis circumference (cm)	Vessel elements (%)	Xylem fibres (%)	Axial parenchyma (%)	Xylem rays (%)
2	12 ( 8-15 )	61 ( 55-67 )	14 ( 10-17 )	13 ( 10-15 )
5	14 ( 12-16 )	50 ( 46-56 )	21 ( 16-24 )	15 ( 11-17 )
10	13 ( 10-17 )	46 ( 44-55 )	26 ( 23-31 )	15 ( 11-17 )
45	13 ( 10-16 )	50 ( 44-55 )	20 ( 18-26 )	17 ( 13-18 )
65	12 ( 8-15 )	44 ( 40-49 )	24 ( 20-28 )	20 ( 16-24 )
90	13 ( 8-15 )	43 ( 40-46 )	22 ( 17-25 )	22 ( 19-24 )
125	16 ( 11-19 )	43 ( 37-48 )	20 ( 17-25 )	21 ( 19-23 )
175	9 ( 7-13 )	56 ( 50-61 )	18 ( 15-24 )	17 ( 14-20 )



TABLE 24

Variation in transectional area occupied by the wood components in the sap wood of Prosonia spicigera in relation to the growing girth of tree axis. The average is based on 320 camera lucida drawings of the wood. Range in parentheses.

Stem axis circumference (cm)	Vessel elements (%)	Xylem fibres (%)	Axial parenchyma (%)	Xylem rays (%)
2	10 ( 7-15 )	23 ( 16-28 )	54 ( 49-59 )	13 ( 11-16 )
5	14 ( 10-16 )	40 ( 32-46 )	32 ( 27-39 )	14 ( 11-16 )
10	15 ( 10-20 )	41 ( 33-46 )	30 ( 26-38 )	14 ( 11-15 )
45	16 ( 11-20 )	50 ( 44-57 )	21 ( 16-26 )	13 ( 9-15 )
65	13 ( 10-18 )	52 ( 46-59 )	21 ( 16-29 )	14 ( 10-15 )
90	12 ( 10-17 )	51 ( 42-55 )	21 ( 20-28 )	16 ( 10-17 )
125	12 ( 7-15 )	58 ( 50-63 )	15 ( 12-18 )	15 ( 12-17 )
175	21 ( 17-24 )	41 ( 37-52 )	20 ( 15-25 )	18 ( 16-23 )

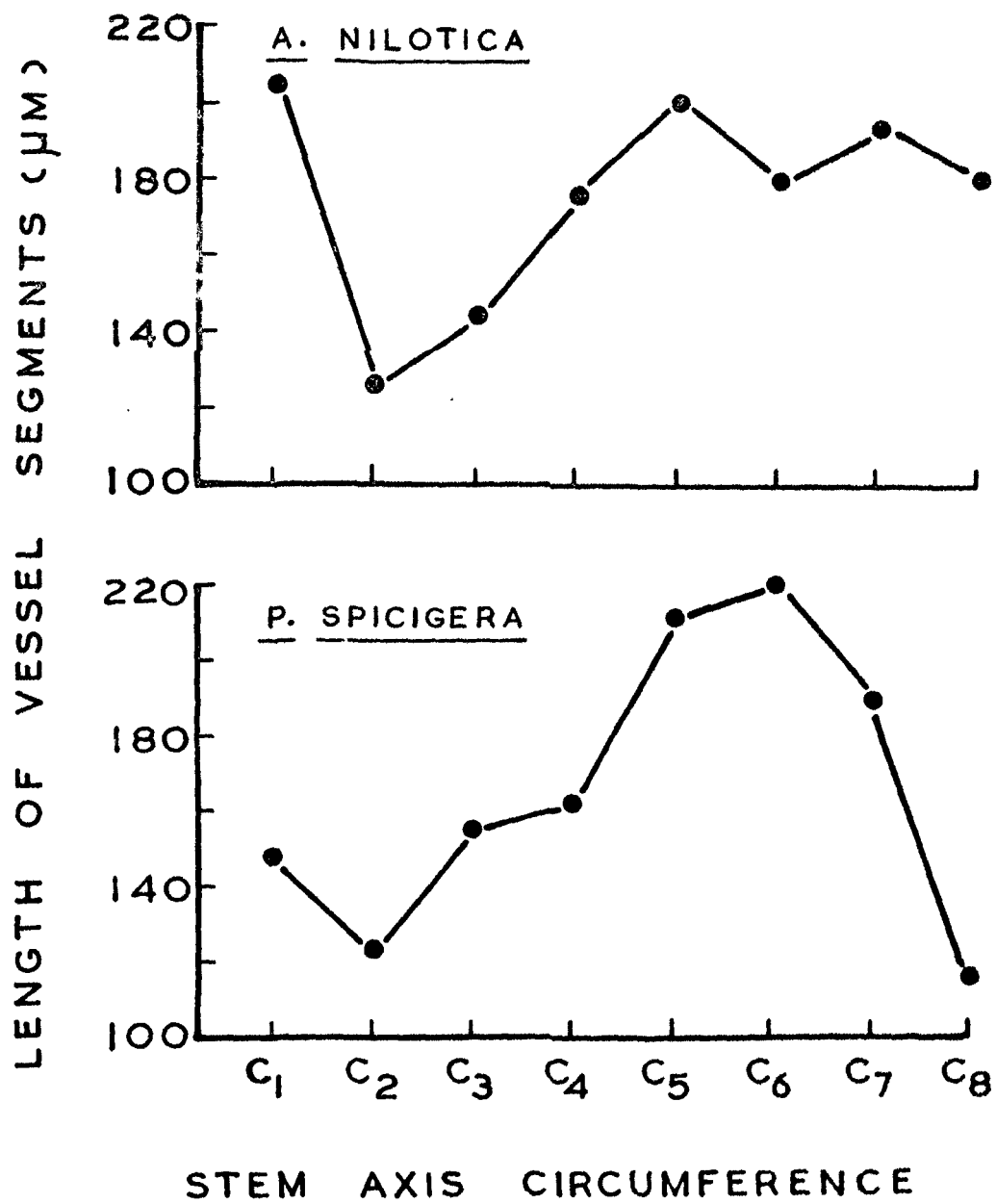


FIG. II

TABLE 25

Size variation of vessel segments in the sap wood of Acacia nilotica in relation to the growing girth of tree axis. The average is based on 1500 independent readings. Range in parentheses.

Stem axis circumference (cm)	Length ( $\mu$ m)	Width ( $\mu$ m)	End wall inclination (degrees)
2	211.6 ( 120-380 )	50.7 ( 19-85 )	73.1 ( 60-85 )
5	126.0 ( 60-228 )	70.2 ( 19-125 )	81.6 ( 64-90 )
10	143.6 ( 60-230 )	25.1 ( 16-50 )	76.8 ( 64-90 )
45	176.2 ( 90-230 )	30.8 ( 16-65 )	75.5 ( 58-88 )
65	200.8 ( 90-300 )	33.9 ( 11-50 )	77.6 ( 60-90 )
90	180.7 ( 60-230 )	45.4 ( 16-85 )	78.1 ( 60-88 )
125	194.1 ( 60-245 )	43.1 ( 25-85 )	70.0 ( 56-86 )
175	180.2 ( 90-260 )	38.2 ( 19-65 )	72.1 ( 56-88 )

**TABLE 26**

Size variation of vessel segments in the sap wood of Prosonia spicigera in relation to the growing girth of tree axis. The average is based on 1600 independent readings. Range in parentheses.

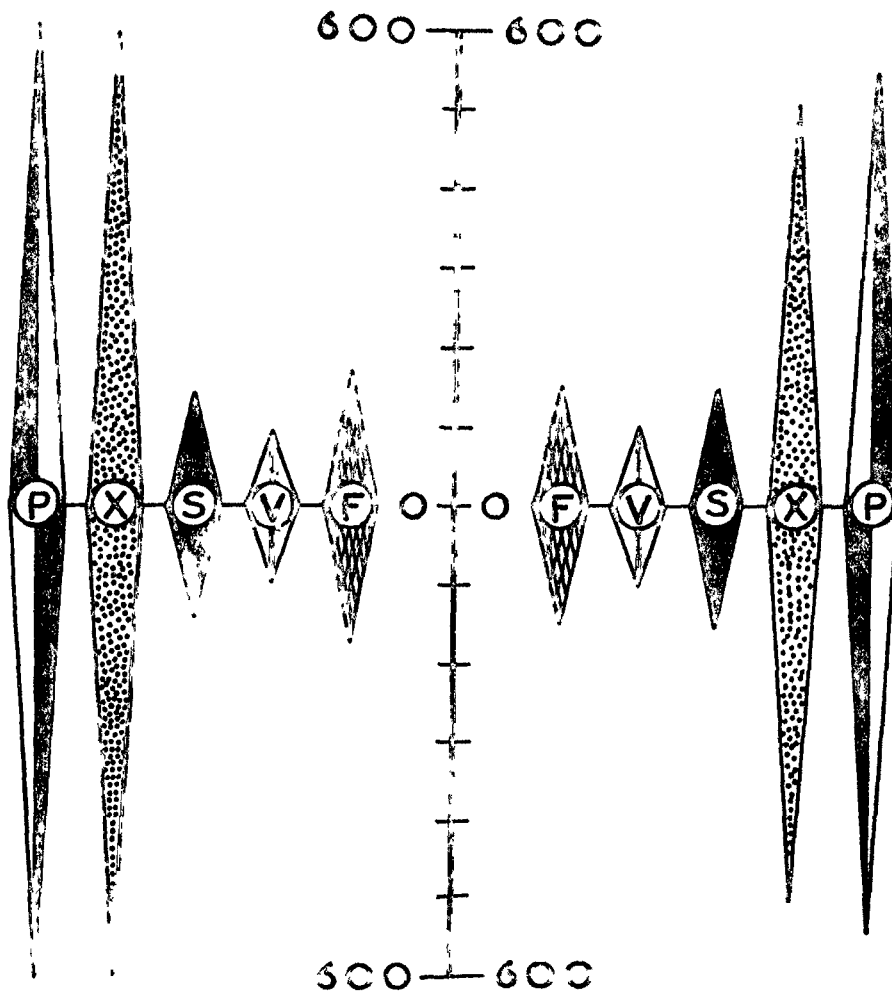
Stem axis circumference (cm)	Length ( $\mu$ m)	Width ( $\mu$ m)	End wall inclination (degrees)
2	148.0 ( 45-225 )	65.2 ( 22-90 )	77.8 ( 62-88 )
5	123.1 ( 30-225 )	74.0 ( 22-120 )	75.8 ( 62-88 )
10	155.4 ( 44-270 )	82.5 ( 15-135 )	77.4 ( 70-88 )
45	163.2 ( 45-270 )	113.0 ( 15-195 )	79.9 ( 63-90 )
65	213.0 ( 75-300 )	109.5 ( 15-180 )	75.4 ( 70-90 )
90	219.5 ( 75-300 )	134.4 ( 15-225 )	71.8 ( 62-88 )
125	190.4 ( 45-270 )	127.0 ( 30-180 )	70.4 ( 58-88 )
175	116.0 ( 45-225 )	156.8 ( 30-205 )	68.8 ( 55-85 )

TABLE 27

Size variation of xylem fibres in the sap wood of Acacia and Prosopis in relation to the growing girth of tree axis. The average is based on 4000 independent readings. Values in parentheses indicate the range.

Stem axis circum- ference(cm)	<u>Acacia nolitica</u>		<u>Prosopis spicigera</u>	
	Fibre length ( $\mu$ m)	Fibre width ( $\mu$ m)	Fibre length ( $\mu$ m)	Fibre width ( $\mu$ m)
2	925.4 ( 480-1350 )	11.4 ( 8-25 )	902.6 ( 480-1280 )	10.4 ( 6-16 )
5	1024.5 ( 480-1550 )	11.8 ( 12-30 )	998.5 ( 480-1550 )	11.0 ( 8-16 )
10	1060.5 ( 560-1550 )	15.2 ( 8-25 )	1044.8 ( 480-1600 )	13.1 ( 8-16 )
45	1056.1 ( 480-1600 )	16.6 ( 10-25 )	968.7 ( 480-1280 )	15.6 ( 12-22 )
65	1078.2 ( 664-1380 )	16.9 ( 8-25 )	1009.0 ( 520-1600 )	16.8 ( 10-24 )
90	1014.4 ( 560-1660 )	14.5 ( 8-22 )	966.6 ( 480-1550 )	14.1 ( 8-22 )
125	1139.6 ( 664-1710 )	17.2 ( 10-35 )	964.6 ( 560-1280 )	13.7 ( 8-16 )
175	1089.3 ( 590-1660 )	15.4 ( 8-25 )	984.8 ( 448-1312 )	14.7 ( 12-20 )

**FIG. 12**



**COMPARATIVE LENGTH OF  
VASCULAR ELEMENTS**

F=FUSIFORM INITIAL    V=VESSEL ELEMENT

S=SIEVE-TUBE MEMBER    X=XYLEM FIBRE

P=PHLOEM FIBRE

SEASONAL VARIATION IN THE STRUCTURE  
OF CAMBIUM AND ITS DERIVATIVE TISSUES

Vascular cambium: The cambium, non-stratified in both the species, also experienced certain seasonal changes both in structure and function. Relative proportion of the two types of cambial initials was noted to differ with seasonal variations. Within a year, the fusiform initials in adult tree trunks constituted about 69-85% and 67-85% of the total tangential area of cambial zone in Acacia and Prosopis respectively. The rest of the cambium in both species was obviously occupied by the ray initials ( Table 28 ) usually grouped into units of diverse shape and size. In Acacia, the amount of fusiform initials was predominant (78-82%) during the grand growth period i.e., from June till September. It was merely 69 to 76% during the other months ( Fig. 13 ). The cambial initials did not exhibit any regular trend of proportional variation in case of Prosopis.

In the active period of cambium the fusiform initials underwent periclinal as well as anticlinal divisions, the former being more frequent during most of the growth period. The anticlinal division was usually dominant during September and October in both the species. After such a division, the

daughter cells used to elongate apically making the two sister cells lie lateral to each other in tangential plane. Depending on the degree of elongation, the elements possessed relatively shorter or longer tapering ends which ranged so widely as from 12 to 168/ $\mu$ m in Acacia and from 16 to 180/ $\mu$ m in Prosonia. Mean length of the ends, however, varied during a year from 45 to 63/ $\mu$ m and from 41 to 64/ $\mu$ m in main trunks of the two species respectively. The mean length of the whole fusiform initial including the tapering ends measured from 294 to 385/ $\mu$ m in the main trunk of Acacia and from 263 to 314/ $\mu$ m in that of Prosonia. Their mean width varied from nearly 15 to 18/ $\mu$ m and from 16 to 18.5/ $\mu$ m in the two species respectively ( Tables 29 & 30 ).

Thus, both the length and width appeared to have been influenced by the prevailing weather conditions. The fusiform initials in Acacia were relatively smaller in size around April. They gained a more or less gradual increase in length till July/August. Having suffered a sharp decline around August and September, their length was noted to regain its previous range of magnitude during winter ( Fig. 14 ). No cognisable variation trend was established for the width of the initials. The length of their tapering ends, however, exhibited a similar variation trend as did the entire body length of the initials in relation to seasonal changes ( Table 29 ).



In case of Proserpia, length of the fusiform initials showed a slight increase from February till June, followed by a slight fall during July and August. In September, however, the length suddenly dropped in all probability due to the onset of anticlinal division. However, the loss was soon made up during the following months ( Fig. 14 ). No such trend was recognized for the width of the initials, albeit it remained slightly less during December-March. Length of the tapering ends measured least during September and October. They showed irregular variation during rest of the year ( Table 30 ).

The ray initials, produced out of the fusiform initials by transverse segmentation or by cutting their lateral or terminal segments, usually grouped together and grew into tall structures by virtue of their repeated divisions. Occasionally, groups of the ray initials were seen fusing together to form tall and broad compound bodies through the conversion of the intervening fusiform initial into a group of the ray initials which formed the bridging connection between the already existing ray initial groups. However, a concomitant splitting of the taller ray units into the smaller ones was also not uncommon.

The heteromorphic ray units in Acacia varied from 1-8 cells in width and from 1-75 cells in height, while in Proserpia

their width and height extended over 1-7 cells and 1-100 cells respectively ( Tables 31-34 ). The mean anticlinal as well as the periclinal diameter of the ray initials varied from 12-15/ $\mu$ m and 14-18/ $\mu$ m in Acacia and from 13-16/ $\mu$ m in Prosonia during the different months of the year ( Table 7 ). A mixed population of the ray units of varying width ( uni to multi-seriate ) and height ( short to tall ) could be observed in one and the same microscopic field. The relative abundance of the units of different dimensions, however, differed periodically.

In Acacia, the multiseriate ray initial units in the adult tree trunk were most frequent ( 23 to 65% ) all the year round. Their abundance was minimum ( 23 to 29% ) in the beginning of active phase i.e., from April to June, and maximum ( 53 to 65% ) during the grand growth period i.e., from July to October. Tetraseriate ray initial units came at the second place and formed about 13 to 25% of the total ray unit population in different months of the year. Here, on the contrary, the minimum abundance ( 13 to 17% ) was found during July to October. The uniseriate, biseriate and triseriate ray initial units formed only 7-15%, 5-21% and 7-21% of the total ray unit population in different months of the year respectively. Their maximum was noted to occur during April

to June. In no case their percentage could exceed 16 during the remaining part of the year ( Table 31 ).

Likewise, the relative abundance of the ray initial units of diverse heights changed with season. The short and medium ray units constituted about 28-45% and 18-36% of the total ray unit population during the different months respectively. Their frequency was found to be minimum (28-33% for the short and 18-23% for the medium ones) in March and later from July till September. The maximum frequency was noted in April. The tall ray initial units (moderately as well as extremely tall units) collectively formed about 19-50% of the total ray unit population during the different months, their minimum being recorded in April and May and later in October and December. None of these categories of the ray units exhibited any regular variation trend of relative abundance with respect to season ( Table 33 ).

In Prosonia, no regular pattern was recognized for the variation in abundance of the ray initial units of varying width with changing seasonal conditions. Mean monthly abundance of the uni, bi, and tri-seriate units varied from 5-16%, 11-19% and 19-47% respectively. The tetraseriate units were usually most abundant, the multiseriate ones being in

considerably smaller proportion, if at all. These two categories collectively constituted about 33-57% of the total number of ray initial units in the cambial zone. Their maximum was noted in April and September, while the minimum in August and October ( Table 32 ).

Similarly, there was a marked variation in the relative abundance of ray initial units of varying heights in different months of a year. The short and medium types of the units constituted about 47-58% and 20-36% of the total ray unit population respectively. The tall ray units, irrespective of their being moderately or extremely tall bodies, could form only 8-32% of the total number of ray units as a whole. Of them, only 0.8-6% fell under the "xtremely tall" category ( Table 34 ). There was hardly a systematic and consistent trend of variation in the frequency of any of the ray-unit types described here. It was, however, noticeable that the number of the short units was minimum during March, June and July. The minimum of the medium type of units was, on the other hand, recorded during the first three months of a calendar year. Conversely, the tall ray units were most frequent from December till May, their occurrence being comparatively meagre in the remaining months ( Table 34 ).

It is to be mentioned here that all the values presented to demonstrate the influence of season on the

cambium and its derivative tissues depict the mean of total observations collected for three consecutive years of the study. The independent sets of readings for the respective calendar years did not show any significant and worth noting differences and more or less tallied with one another.

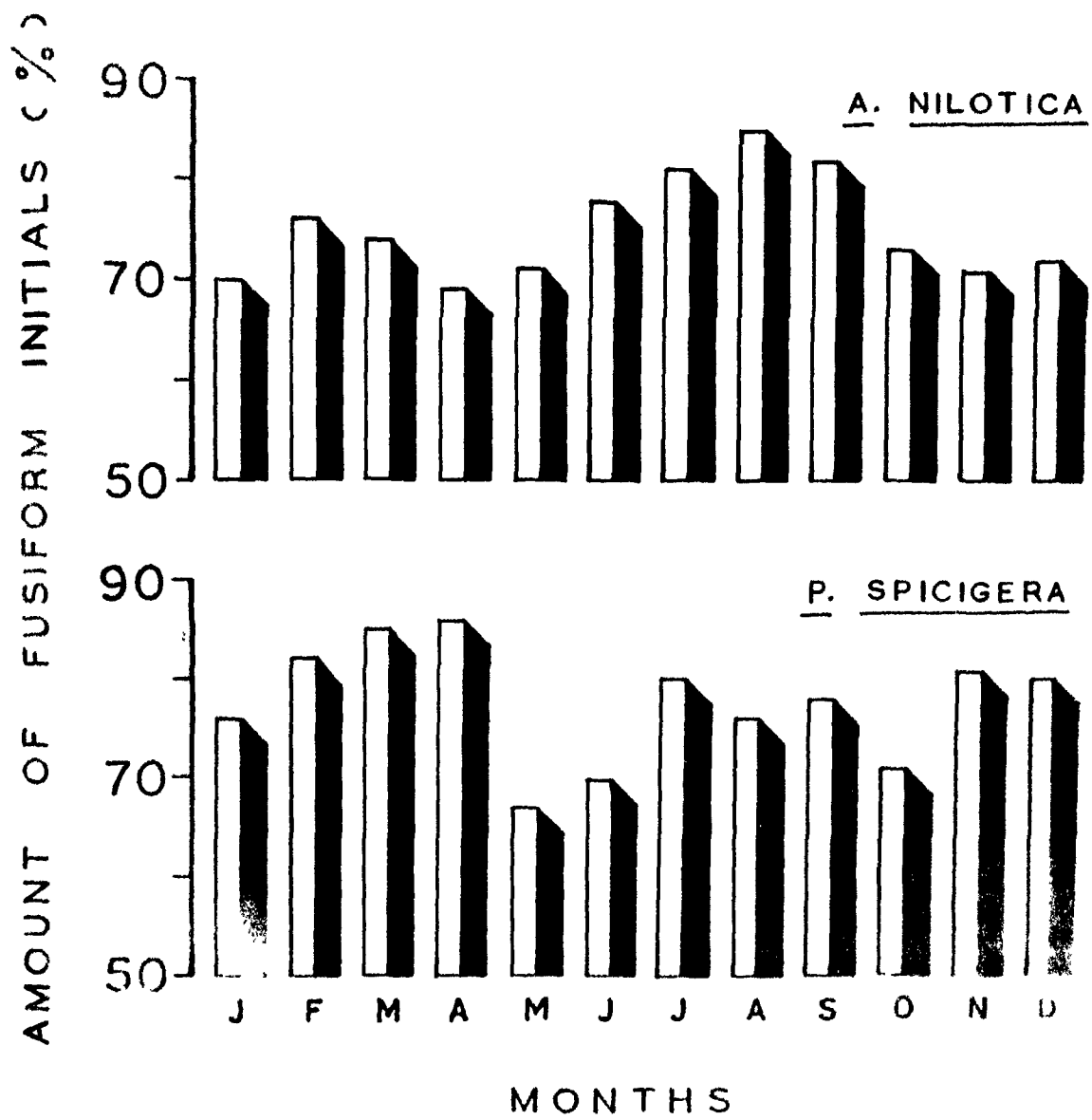


FIG.13

TABLE 28

Seasonal variation in the relative proportion of fusiform and ray initials in Acacia nilotica and Prosopis spiciqera. The average is based on 240 camera lucida drawings of the cambial initials. Values in parentheses indicate the range.

Months	<u>Acacia nilotica</u>		<u>Prosopis spiciqera</u>	
	Fusiform initials (%)	Ray inititals (%)	Fusiform initials (%)	Ray initials (%)
January	70 ( 65-72 )	30 ( 28-33 )	76 ( 72-80 )	24 ( 20-26 )
February	76 ( 74-79 )	24 ( 20-28 )	82 ( 80-85 )	18 ( 16-21 )
March	74 ( 70-78 )	26 ( 22-28 )	85 ( 80-90 )	15 ( 14-20 )
April	69 ( 65-72 )	31 ( 28-35 )	86 ( 74-79 )	24 ( 21-30 )
May	71 ( 68-75 )	29 ( 26-33 )	67 ( 65-70 )	33 ( 30-38 )
June	78 ( 75-80 )	22 ( 20-26 )	70 ( 65-74 )	30 ( 25-35 )
July	81 ( 80-83 )	19 ( 16-22 )	80 ( 75-84 )	20 ( 16-25 )
August	85 ( 80-87 )	15 ( 13-20 )	76 ( 71-79 )	24 ( 21-29 )
September	82 ( 89-85 )	18 ( 15-20 )	78 ( 75-80 )	22 ( 20-26 )
October	73 ( 71-75 )	27 ( 25-30 )	71 ( 65-75 )	29 ( 25-34 )
November	71 ( 70-75 )	29 ( 25-32 )	81 ( 78-85 )	19 ( 16-22 )
December	72 ( 68-75 )	28 ( 25-32 )	80 ( 78-85 )	20 ( 16-25 )

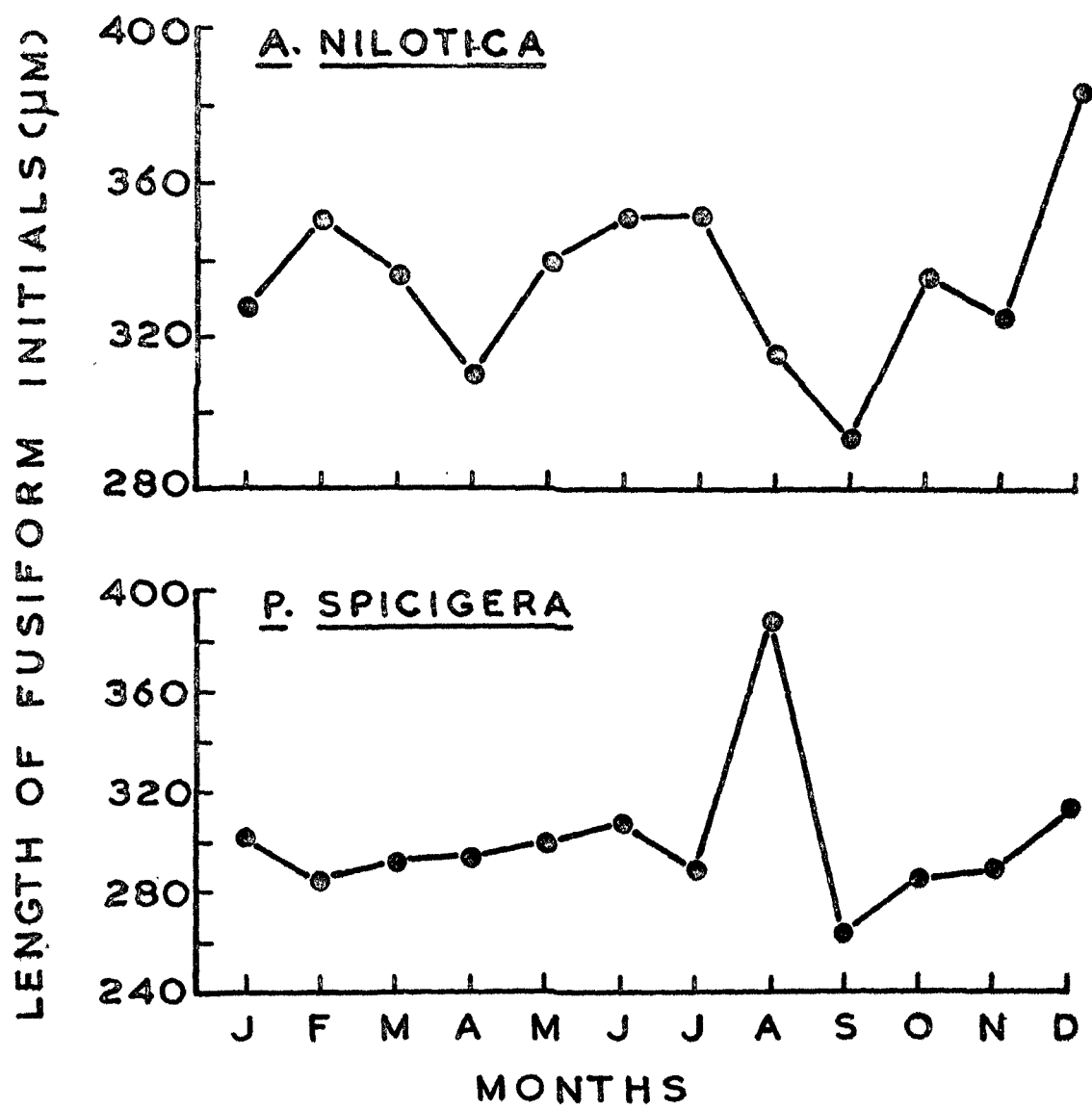


FIG. 14



TABLE 29

Seasonal variation in size of fusiform initials of Acacia pilotica. Values presented indicate the mean of 2400 independent readings. Range is given in parentheses.

Months	Fusiform initials		
	Length (/um)	width (/um)	Tapering end (/um)
January	328.0 ( 182-418 )	16.8 ( 11-21 )	58.1 ( 20-152 )
February	350.6 ( 250-430 )	17.1 ( 11-26 )	50.1 ( 16-160 )
March	338.2 ( 226-411 )	16.6 ( 13-23 )	48.2 ( 16-150 )
April	310.7 ( 228-418 )	16.8 ( 11-23 )	51.8 ( 16-156 )
May	340.2 ( 226-456 )	17.2 ( 13-28 )	61.8 ( 23-165 )
June	351.1 ( 265-478 )	17.0 ( 15-27 )	59.2 ( 20-160 )
July	352.7 ( 182-486 )	17.7 ( 11-27 )	62.9 ( 18-168 )
August	316.5 ( 228-418 )	16.7 ( 13-21 )	56.2 ( 20-120 )
September	294.1 ( 142-478 )	15.2 ( 11-23 )	47.9 ( 12-120 )
October	338.8 ( 130-411 )	16.3 ( 11-23 )	45.1 ( 20-150 )
November	326.8 ( 152-608 )	17.5 ( 15-23 )	56.8 ( 12-150 )
December	385.8 ( 265-478 )	17.3 ( 13-27 )	54.9 ( 16-120 )

TABLE 30

Seasonal variation in size of fusiform initials of Prosopis spicigera. Values presented indicate the mean of 2400 independent readings. Range in parentheses.

Months	Fusiform initials		
	Length (/um)	width (/um)	Tapering end (/um)
January	302.2 ( 228-411 )	16.0 ( 12-24 )	60.7 ( 20-158 )
February	286.9 ( 152-380 )	16.2 ( 12-24 )	59.8 ( 26-152 )
March	292.3 ( 228-390 )	15.9 ( 11-24 )	64.0 ( 40-180 )
April	294.0 ( 224-400 )	17.0 ( 12-24 )	59.1 ( 28-160 )
May	300.8 ( 240-380 )	16.8 ( 11-27 )	49.0 ( 20-120 )
June	308.2 ( 240-428 )	17.2 ( 12-27 )	50.1 ( 20-128 )
July	289.1 ( 224-380 )	17.9 ( 12-24 )	54.8 ( 30-152 )
August	389.8 ( 184-390 )	17.3 ( 11-28 )	58.7 ( 16-160 )
September	263.0 ( 150-320 )	16.4 ( 11-28 )	44.1 ( 16-180 )
October	286.5 ( 268-340 )	18.4 ( 14-28 )	40.8 ( 16-128 )
November	290.4 ( 226-418 )	17.2 ( 12-21 )	55.1 ( 26-156 )
December	314.2 ( 248-411 )	16.3 ( 12-24 )	51.8 ( 20-156 )

TABLE 31

Seasonal variation in the relative abundance of ray initial units of varying width in the cambium of Acacia nilotica. The average is based on readings from 960 microscopic fields. Range is given in parentheses.

Months	Maximum width (No. of cells)	Uni-seriate (%)	Bi-seriate (%)	Tri-seriate (%)	Tetra-seriate (%)	Multi-seriate (%)
January	7	8 ( 4-11)	13 (10-17)	13 (10-16)	20 (17-24)	46 (39-49)
February	7	10 ( 6-13)	12 (10-16)	15 (12-17)	21 (18-24)	42 (38-46)
March	6	7 ( 4-12)	10 ( 5-13)	16 (13-20)	24 (19-26)	43 (38-45)
April	5	15 (10-17)	16 (14-20)	18 (14-22)	22 (20-25)	29 (28-33)
May	6	13 (10-17)	20 (16-23)	19 (14-21)	21 (19-25)	27 (24-29)
June	8	12 (10-15)	21 (20-23)	21 (19-24)	23 (20-25)	23 (20-25)
July	7	7 ( 4-10)	12 ( 9-15)	11 ( 9-15)	17 (14-20)	53 (48-58)
August	7	11 ( 8-15)	13 (10-15)	8 ( 4-10)	14 (12-17)	54 (51-58)
September	7	10 ( 7-15)	7 ( 4-12)	7 ( 4-10)	13 (10-15)	63 (60-68)
October	7	7 ( 4-11)	5 ( 3-8 )	7 ( 5-10)	16 (11-20)	65 (61-68)
November	6	8 ( 4-11)	11 ( 8-14)	14 (12-17)	25 (20-28)	42 (40-46)
December	6	8 ( 5-11)	12 ( 8-16)	12 ( 9-14)	22 (20-26)	46 (42-51)

TABLE 32

Seasonal variation in the relative abundance of ray initial units of varying width in the cambium of Prosopis spicigera. The average is based on readings from 960 microscopic fields. Range is given in parentheses.

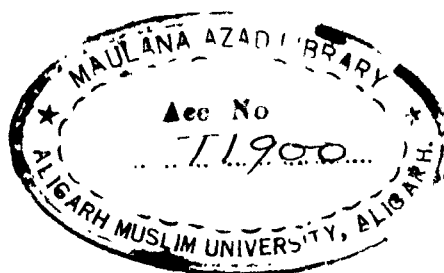
Months	Maximum width (No. of cells)	Uni- seriate (%)	Bi- seriate (%)	Tri- seriate (%)	Tetra- seriate (%)	Multi- seriate (%)
January	6	15 (12-19)	15 (13-18)	21 (18-26)	36 (34-39)	13 (10-15)
February	6	14 (12-19)	16 (13-18)	20 (13-23)	40 (35-44)	10 ( 7-12)
March	5	12 (10-16)	17 (15-21)	27 (22-30)	42 (40-46)	2 ( 1-5 )
April	5	7 ( 4-9 )	12 (10-16)	24 (21-30)	55 (52-58)	2 ( 1-5 )
May	5	10 ( 8-12)	11 ( 8-16)	29 (27-33)	47 (45-52)	3 ( 1-7 )
June	6	16 (14-20)	18 (16-21)	26 (22-29)	24 (20-27)	16 (14-19)
July	7	12 (10-15)	19 (16-21)	27 (25-30)	29 (26-31)	13 (10-17)
August	7	15 (12-18)	18 (15-20)	31 (25-34)	23 (20-25)	13 (10-15)
September	5	9 ( 5-11)	15 (12-20)	19 (16-25)	54 (51-58)	3 ( 1-5 )
October	4	5 ( 3-8 )	15 (11-20)	47 (43-50)	33 (31-36)	-
November	5	10 ( 6-15)	14 (12-20)	27 (24-30)	44 (40-48)	5 ( 1-7 )
December	5	7 ( 4-11)	15 (12-21)	31 (24-34)	45 (42-50)	2 ( 1-5 )

**TABLE 33**

Seasonal variation in the relative abundance of the ray initial units of varying height in the cambium of *Acacia nilotica*. The average is based on readings from 960 microscopic fields. Range is given in parentheses.

Months	Maximum height (No. of cells)	Short (1-5 cells)	Medium (16-30 cells)	Tall	
				Moderate (31-45 cells)	Extreme (Above 45 cells)
January	70	40 ( 37-45 )	26 ( 21-30 )	20 ( 16-24 )	14 ( 10-18 )
February	68	36 ( 34-40 )	28 ( 25-34 )	26 ( 20-30 )	10 ( 8-13 )
March	78	33 ( 30-35 )	22 ( 19-25 )	29 ( 25-36 )	16 ( 14-18 )
April	75	45 ( 40-49 )	36 ( 32-40 )	11 ( 9-15 )	8 ( 6-10 )
May	70	42 ( 40-46 )	33 ( 30-40 )	19 ( 16-25 )	6 ( 5-10 )
June	70	34 ( 30-37 )	32 ( 30-40 )	24 ( 20-27 )	10 ( 7-15 )
July	70	28 ( 25-32 )	23 ( 20-27 )	36 ( 34-40 )	13 ( 10-16 )
August	68	30 ( 26-35 )	20 ( 17-25 )	36 ( 30-40 )	14 ( 10-16 )
September	60	33 ( 30-35 )	18 ( 15-22 )	39 ( 35-44 )	10 ( 8-16 )
October	70	44 ( 40-49 )	29 ( 25-35 )	19 ( 16-22 )	8 ( 5-10 )
November	55	40 ( 38-46 )	25 ( 20-31 )	22 ( 20-25 )	13 ( 11-18 )
December	65	42 ( 38-45 )	28 ( 24-35 )	18 ( 15-25 )	12 ( 10-14 )

**TABLE 34**



Seasonal variation in the relative abundance of the ray initial units of varying height in the cambium of Prosopis spicigera. The average is based on readings from 960 microscopic fields. Range is given in parentheses.

Months	Maximum height (No. of cells)	Short (1-5 cells)	Medium (16-30 cells)	Tall	
				Moderate (31-45 cells)	Extreme (above 45 cells)
January	70	56 ( 50-60 )	22 ( 18-27 )	20 ( 16-27 )	2 ( 1-5 )
February	80	54 ( 50-60 )	22 ( 18-26 )	21 ( 16-26 )	3 ( 1-5 )
March	83	48 ( 45-51 )	20 ( 18-25 )	26 ( 22-30 )	6 ( 1-8 )
April	90	55 ( 50-60 )	27 ( 25-30 )	16 ( 12-20 )	2 ( 1-5 )
May	78	50 ( 46-53 )	28 ( 25-33 )	20 ( 18-25 )	2 ( 1-4 )
June	80	47 ( 45-50 )	36 ( 30-40 )	13 ( 10-15 )	4 ( 2-6 )
July	93	48 ( 45-54 )	36 ( 32-40 )	12 ( 10-15 )	4 ( 2-7 )
August	100	59 ( 55-61 )	32 ( 30-36 )	7 ( 4-10 )	2 ( 1-5 )
September	96	54 ( 50-58 )	29 ( 26-32 )	14 ( 12-20 )	3 ( 1-5 )
October	70	58 ( 55-60 )	34 ( 30-40 )	7 ( 4-11 )	1 ( 0-3 )
November	80	50 ( 47-55 )	36 ( 34-40 )	13 ( 10-16 )	1 ( 0-4 )
December	65	50 ( 46-55 )	30 ( 27-35 )	18 ( 13-21 )	2 ( 1-4 )

Secondary phloem: A derivative of the non-stratified cambium, the phloem also mirrored the same fashion of cell arrangement. The non-storied pattern of both the rays and sieve-tube members was manifest in tangential-longitudinal view.

In Acacia, the over all thickness of the secondary phloem varied a little ( 8.94 mm - 11.32 mm ) during a calendar year because of the combined influence of periderm at the periphery and vascular cambium at the inner boundary. The conducting zone of the phloem measured from 1.32 to 2.32 mm during the different months, leaving the non-conducting one to vary from 7.27 to 9.00 mm. The conducting zone remained relatively narrow during winters with its minimum width around February, and grew thicker during summers with the maximum in September ( Table 35 ).

Microscopic analysis of the conducting phloem brought out that the proportion of the different phloem components in transections also differed to certain extent with the change in season. The area of sieve-tube members, phloem fibres, axial parenchyma and phloem rays varied from 50-59%, 16-20%, 5-15% and 16-18% respectively ( Table 37 ). No systematic trend of variation was observed for any of these components during a calendar year. The area of sieve-tube members, however, tended to be slightly greater during summer than in the remaining part of a year.

The microscopic examination of the sieve-tube members also revealed certain changes in their dimensions under the seasonal influence. The mean length and width of the elements varied during a calendar year from 244.6 to 323.9/ $\mu$ m and from 20.2 to 27.2/ $\mu$ m respectively ( Table 39 ). It was noted that the length had been a little bit suppressed during the early months of the year, the minimum being recorded in March. From June onwards, the mean length varied from 284 to 323/ $\mu$ m, the maximum being noted in October ( Fig. 15 ). The variation in width was somewhat irregular and unsystematic. The minimum and maximum width was found in April and October respectively. Angle of inclination of the sieve-tube end walls was also observed in relation to season. Their average inclination ranged between 30.5 and 43.2 degrees. Although the variation was not very gradual and consistent, it was noteworthy that the angle of inclination increased during summer, and from July till January it declined almost continuously ( Table 39 ).

Similarly, the dimensional variation in relation to season was investigated for fibre elements, the other important constituent of the phloem. They varied in their mean length and width from 1046 to 1345/ $\mu$ m and from 15.5 to 18.0/ $\mu$ m respectively. The variation was not gradual. However, the fibres appeared to be comparatively shorter during summer, more specifically from June till September ( Table 41 ).



A similar investigation with Prosonia elucidated that the total thickness of secondary phloem averaged to be 1.92 mm to 3.84 mm in different months of a calendar year. Of this, about 0.50 to 1.10 mm used to function as the conducting zone, the remainder forming the non-conducting phloem. The conducting zone was relatively wider from May till September. The non-conducting region varied in thickness irregularly ( Table 36 ).

Further, the estimation of relative proportion of the various components of conducting phloem in this species demonstrated an irregular variation pattern. During a calendar year, the average proportion of sieve-tube members and phloem fibres, as seen in transections, varied from 21 to 41% and 15 to 35% respectively. Likewise, the proportion of axial parenchyma and phloem rays constituted about 20 to 30% and 15 to 18% of the conducting phloem respectively during the different months ( Table 38 ).

As regards the size variation of sieve-tube members and phloem fibres in Prosonia, it is not very gradual and systematic. It is evident from the data presented in Table 40 that the mean monthly variation in length and width of the sieve-tube members during the years of study extended from 281.7 to 310.8/ $\mu$ m and from 21.0 to 28.4/ $\mu$ m respectively. The minimum length was recorded in September while the maximum

in December ( Fig. 15 ). Inclination of sieve-tube end walls was slightly greater from March till June ( 32.9 to 34.2°), the over all variation during a year ranging from 26.4 to 34.2 degrees ( Table 40 ). In the case of phloem fibres, the mean length varied from nearly 1030/ $\mu$ m to 1157/ $\mu$ m, while the width from 15.7/ $\mu$ m to 18.1/ $\mu$ m. The average fibre length tended to be greater from October till May and smaller from June to September with some minor fluctuations, of course. Width variation was not much significant ( Table 41 ).

TABLE 35

Seasonal variation in thickness of secondary phloem and its component zones in Acacia nilotica.

Months	Total secondary phloem (mm)	Conducting phloem (mm)	Non-conducting phloem (mm)
January	9.13	1.51	7.62
February	9.44	1.32	8.12
March	9.67	1.61	8.06
April	10.19	1.69	8.50
May	9.77	1.81	7.96
June	9.82	1.80	8.02
July	9.40	1.90	7.50
August	10.01	1.96	8.05
September	11.32	2.32	9.00
October	10.72	2.16	8.56
November	9.44	1.94	7.50
December	8.94	1.67	7.27

TABLE 36

Seasonal variation in thickness of secondary phloem and its component zones in Prosopis spicigera.

Months	Total secondary phloem (mm)	Conducting phloem (mm)	Non-conducting phloem (mm)
January	2.04	0.50	1.54
February	2.11	0.61	1.50
March	2.50	0.60	1.90
April	2.41	0.75	1.66
May	2.56	0.92	1.64
June	2.64	1.03	1.61
July	2.09	1.10	0.99
August	2.70	1.04	1.66
September	3.85	0.86	2.99
October	2.64	0.55	1.99
November	1.92	0.58	1.34
December	2.03	0.56	1.47

TABLE 37

Seasonal variation in transectional area occupied by different phloic components in the conducting phloem of Acacia nilotica. The average is based on 240 camera lucida drawings of the phloem. Range is given in parentheses.

Months	Sieve-tube members (%)	Phloem fibres (%)	Axial Parenchyma (%)	Phloem rays (%)
January	51 ( 45-56 )	18 ( 16-22 )	13 ( 10-15 )	18 ( 14-20 )
February	52 ( 44-55 )	17 ( 14-22 )	13 ( 10-16 )	18 ( 14-22 )
March	52 ( 48-58 )	18 ( 14-23 )	14 ( 10-16 )	16 ( 11-20 )
April	50 ( 42-56 )	17 ( 14-24 )	15 ( 11-20 )	18 ( 15-22 )
May	53 ( 48-60 )	16 ( 12-20 )	14 ( 11-18 )	17 ( 14-20 )
June	51 ( 45-62 )	18 ( 12-22 )	13 ( 10-20 )	18 ( 14-21 )
July	59 ( 52-62 )	20 ( 16-25 )	05 ( 4-10 )	16 ( 13-22 )
August	53 ( 50-59 )	17 ( 14-20 )	13 ( 10-18 )	17 ( 14-20 )
September	53 ( 49-59 )	17 ( 12-20 )	14 ( 10-18 )	16 ( 12-20 )
October	51 ( 48-58 )	18 ( 15-24 )	14 ( 11-18 )	17 ( 15-20 )
November	52 ( 44-58 )	17 ( 13-22 )	13 ( 10-16 )	18 ( 14-23 )
December	51 ( 47-56 )	18 ( 15-24 )	14 ( 12-18 )	17 ( 14-19 )

TABLE 38

Seasonal variation in transectional area occupied by different phloic components in the conducting phloem of Prosopis spicigera. The average is based on 240 camera lucida drawings of the phloem. Range is given in parentheses.

Months	Sieve-tube elements (%)	Phloem fibres (%)	Axial parenchyma (%)	Phloem rays (%)
January	37 ( 32-40 )	26 ( 21-32 )	21 ( 16-26 )	16 ( 12-20 )
February	35 ( 30-39 )	28 ( 22-30 )	20 ( 16-27 )	17 ( 14-20 )
March	38 ( 35-40 )	20 ( 16-25 )	26 ( 22-31 )	16 ( 14-21 )
April	41 ( 36-45 )	15 ( 12-18 )	29 ( 25-35 )	15 ( 12-20 )
May	36 ( 32-40 )	18 ( 16-21 )	30 ( 28-36 )	16 ( 12-20 )
June	31 ( 25-36 )	24 ( 21-30 )	28 ( 24-31 )	17 ( 13-20 )
July	27 ( 24-35 )	28 ( 25-30 )	27 ( 24-32 )	18 ( 15-20 )
August	21 ( 17-25 )	35 ( 30-40 )	26 ( 20-28 )	18 ( 14-20 )
September	33 ( 30-38 )	28 ( 25-35 )	24 ( 20-28 )	15 ( 12-18 )
October	29 ( 25-34 )	34 ( 30-39 )	22 ( 18-26 )	15 ( 12-19 )
November	32 ( 30-36 )	25 ( 20-28 )	26 ( 22-30 )	17 ( 14-20 )
December	30 ( 27-35 )	27 ( 25-30 )	26 ( 20-30 )	17 ( 14-22 )

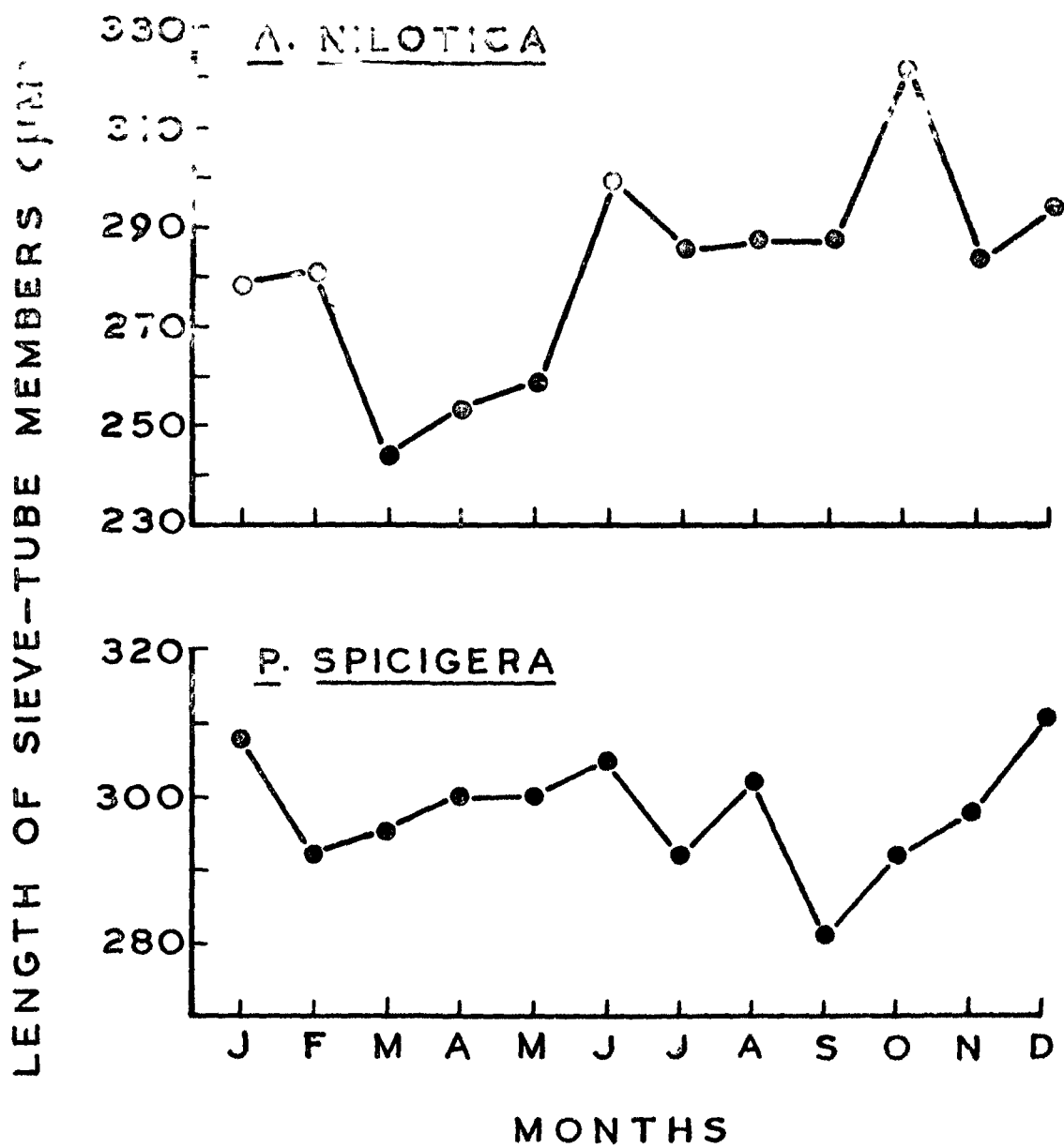


FIG. 15

TABLE 32

Seasonal variation in size of sieve-tube members in the conducting phloem of *Acacia nilotica*. The average is based on 2400 independent readings. Values in parentheses indicate the range.

Months	Length ( $\mu$ m)	Width ( $\mu$ m)	End wall inclination (degrees)
January	278.2 ( 152-350 )	25.4 ( 18-30 )	30.5 ( 15-50 )
February	281.0 ( 133-350 )	26.2 ( 22-35 )	34.6 ( 15-60 )
March	244.6 ( 144-364 )	20.8 ( 11-30 )	33.0 ( 15-60 )
April	253.0 ( 126-350 )	20.2 ( 11-27 )	40.1 ( 20-80 )
May	259.6 ( 126-338 )	22.7 ( 15-34 )	43.2 ( 20-68 )
June	299.2 ( 216-380 )	20.9 ( 11-30 )	38.4 ( 20-70 )
July	286.6 ( 114-437 )	21.7 ( 15-27 )	39.5 ( 15-75 )
August	288.2 ( 176-350 )	24.9 ( 15-34 )	36.1 ( 15-60 )
September	287.7 ( 209-388 )	22.4 ( 15-30 )	33.8 ( 15-50 )
October	323.9 ( 152-418 )	27.2 ( 22-30 )	34.1 ( 15-50 )
November	284.4. ( 133-304 )	23.0 ( 15-27 )	31.9 ( 15-60 )
December	296.5 ( 190-331 )	26.8 ( 22-38 )	31.3 ( 18-60 )



TABLE 40

Seasonal variation in size of sieve-tube members in the conducting phloem of Prosopis spicigera. The average is based on 2400 independent readings. Values in parentheses indicate the range.

Months	Length (/um)	Width (/um)	End wall inclination (degrees)
January	308.4 ( 214-370 )	23.6 ( 18-30 )	30.1 ( 10-42 )
February	292.2 ( 190-354 )	21.9 ( 17-34 )	28.3 ( 10-45 )
March	295.0 ( 186-350 )	22.9 ( 17-39 )	32.9 ( 15-70 )
April	299.8 ( 210-367 )	28.4 ( 18-45 )	34.2 ( 16-81 )
May	299.9 ( 170-386 )	24.8 ( 15-30 )	33.6 ( 16-75 )
June	305.1 ( 195-390 )	26.9 ( 17-39 )	33.3 ( 15-75 )
July	292.3 ( 156-367 )	25.1 ( 17-45 )	27.7 ( 12-50 )
August	298.4 ( 170-370 )	23.2 ( 18-39 )	28.5 ( 12-52 )
September	281.7 ( 136-350 )	21.0 ( 17-39 )	26.4 ( 15-42 )
October	292.1 ( 170-367 )	22.9 ( 14-34 )	27.8 ( 15-52 )
November	298.2 ( 196-386 )	24.6 ( 15-39 )	26.9 ( 12-70 )
December	310.8 ( 210-370 )	26.7 ( 18-39 )	27.0 ( 16-50 )

**TABLE 41**

Seasonal variation in size of phloem fibres in Acacia and Prosopis. The average is based on 4800 independent readings. Values in parentheses indicate the range.

Months	<u>Acacia nilotica</u>		<u>Prosopis spicigera</u>	
	Fibre length (/um)	Fibre width (/um)	Fibre length (/um)	Fibre width (/um)
January	1129.2 ( 320-3400 )	16.3 ( 4-28 )	1096.0 ( 320-2560 )	16.6 ( 8-26 )
February	1345.0 ( 520-3200 )	17.8 ( 4-30 )	1120.8 ( 420-2480 )	18.1 ( 8-30 )
March	1269.5 ( 500-3200 )	18.0 ( 8-32 )	1089.8 ( 360-3020 )	16.9 ( 8-20 )
April	1198.7 ( 400-3200 )	17.2 ( 8-28 )	1101.9 ( 380-2560 )	17.0 ( 4-28 )
May	1160.4 ( 385-2560 )	16.1 ( 8-26 )	1116.2 ( 400-3200 )	17.7 ( 8-26 )
June	1109.3 ( 320-2450 )	16.2 ( 8-26 )	1036.8 ( 320-2450 )	15.7 ( 4-22 )
July	1169.1 ( 380-2560 )	15.5 ( 8-24 )	1030.2 ( 400-2200 )	16.4 ( 4-24 )
August	1086.2 ( 380-3010 )	15.9 ( 5-24 )	1046.9 ( 480-1440 )	16.8 ( 8-24 )
September	1046.5 ( 320-2450 )	16.0 ( 4-28 )	1062.9 ( 500-1860 )	16.8 ( 8-26 )
October	1121.9 ( 380-3200 )	16.7 ( 4-32 )	1148.2 ( 480-2450 )	16.6 ( 8-26 )
November	1154.2 ( 380-3010 )	16.8 ( 8-32 )	1122.4 ( 320-2200 )	17.2 ( 4-30 )
December	1114.7 ( 380-3200 )	16.2 ( 4-28 )	1157.3 ( 550-3150 )	16.9 ( 8-28 )

Secondary xylem: Analysis of transections of the sap wood from adult tree trunks has brought to light that the relative proportion of the various xylem components also varies considerably with changes in season. It was observed in Acacia that vessel elements formed about 12 to 34% of the sap wood during the different months. The minimum amount was noted to occur from April to June as well as in December. The proportion remained appreciably higher from July till October. Contrary to this, the proportion of xylem fibres was comparatively lower ( 34-48% ) during this period i.e., from July till October, and considerably higher ( 56-68% ) during rest of the year. On the other hand, the seasonal variation in the amount of axial parenchyma and xylem rays did not portray any regular and systematic trend. Their proportion, however, hovered around 9-18% and 11-16% respectively ( Table 42 ).

In addition to this, the influence of season was also noticed on the size of vessel segments and xylem fibres, the main component elements of the wood. Mean length of the vessel segments was found to vary in the different months from 176.4 to 221.2/ $\mu$ m, with its minimum and maximum falling around January and June respectively. The length was somewhat depressed during winter ( October-March ) while it tended to increase in summer i.e., from April till September ( Fig. 16 ). As evident from Table 44, the mean width of

the segments also followed a more or less similar variation pattern with some occasional irregularities. It varied from 30.6/ $\mu$ m ( January ) to 51.7/ $\mu$ m ( August ). The xylem fibres varied in their main length and width from 1090.2 to 1321/ $\mu$ m and from 14.6 to 17.8/ $\mu$ m respectively. Both the mean length as well as the mean width was noticed to be minimum in December and maximum in September ( Table 46 ).

In case of Prosopis, the vessel segments constituted about 15-32% of the conducting xylem in transections in the different months of a calendar year. The maximum amount ( 22-32% ) was observed during March, April and May. Rest of the year their proportion stayed more or less constant and lay around 15 to 18%. Further, the xylem fibres formed about 22 to 56% of the total sap wood. Here, on the contrary, the minimum amount ( 22-44% ) was found during March, April and May, while the proportion was relatively higher ( 48-56% ) during the remaining months. The relative proportions of axial parenchyma and xylem rays varied during a calendar year from 12-30% and 14-16% respectively. Again in this species too, both of these components varied irregularly showing no consistent variation trend ( Table 43 ).

As to the matter of cell size variation in relation to season, the vessel segments and the fibres were influenced

most. The vessel segments varied in their mean length and width from 128.6 to 224.2/ $\mu$ m and from 98 to 156.3/ $\mu$ m respectively ( Table 45 ). Length of the segments remained relatively greater during winter and early spring i.e., from December till April. It attained its maximum in December ( Fig. 16 ). Width of the segments, however, did not portray any cognizable trend of seasonal variation.

The data presented in Table 46 indicate that the xylem fibres too did not evince any systematic variation in length or width. The two dimensions were noted to measure from 944.5 to 1090.0/ $\mu$ m and from 13.8 to 16.9/ $\mu$ m respectively ( Table 46 ).

The dimensional changes were incongruous as well as insignificant in case of axial and ray parenchyma in both the species studied.

TABLE 42

Seasonal variation in the relative amount (transectional area) of the different wood components in Acacia nilotica. The average is based on 240 camera lucida drawings of the wood. Values in parentheses indicate the range.

Months	Vessel elements (%)	Xylem fibres (%)	Axial parenchyma (%)	Xylem rays (%)
January	14 ( 10-18 )	57 ( 53-60 )	15 ( 12-19 )	14 ( 10-18 )
February	13 ( 10-18 )	56 ( 53-60 )	16 ( 12-18 )	15 ( 12-17 )
March	14 ( 10-17 )	59 ( 55-65 )	13 ( 10-17 )	14 ( 12-18 )
April	12 ( 9-16 )	61 ( 58-65 )	15 ( 11-20 )	12 ( 10-15 )
May	12 ( 9-15 )	60 ( 53-64 )	16 ( 12-20 )	12 ( 9-14 )
June	12 ( 10-16 )	68 ( 65-74 )	9 ( 6-14 )	11 ( 8-14 )
July	34 ( 28-39 )	34 ( 30-39 )	16 ( 12-21 )	16 ( 12-20 )
August	24 ( 20-27 )	43 ( 39-48 )	17 ( 12-20 )	16 ( 13-19 )
September	21 ( 19-25 )	46 ( 42-51 )	18 ( 14-23 )	15 ( 14-18 )
October	20 ( 17-24 )	48 ( 45-55 )	18 ( 15-24 )	14 ( 12-20 )
November	14 ( 10-18 )	59 ( 55-63 )	15 ( 12-22 )	12 ( 10-15 )
December	12 ( 7-15 )	56 ( 50-60 )	18 ( 15-22 )	14 ( 12-20 )

**TABLE 43**

Seasonal variation in the relative amount (based on transectional area) of the different wood components in *Prosonia spicigera*. The average is based on 240 camera lucida drawings of the wood. Values in parentheses indicate the range.

Months	Vessel elements (%)	Xylem fibres (%)	Axial parenchyma (%)	Xylem rays (%)
January	16 ( 12-19 )	55 ( 51-59 )	16 ( 12-19 )	14 ( 9-17 )
February	18 ( 16-21 )	48 ( 44-51 )	20 ( 18-23 )	14 ( 11-18 )
March	22 ( 16-25 )	44 ( 40-46 )	18 ( 12-21 )	16 ( 14-21 )
April	32 ( 30-39 )	22 ( 20-27 )	30 ( 24-35 )	16 ( 12-20 )
May	26 ( 21-31 )	39 ( 33-42 )	20 ( 15-27 )	15 ( 12-20 )
June	17 ( 15-20 )	53 ( 50-59 )	14 ( 10-19 )	16 ( 10-20 )
July	18 ( 15-21 )	50 ( 46-55 )	18 ( 14-21 )	14 ( 10-19 )
August	16 ( 12-19 )	51 ( 45-62 )	18 ( 15-20 )	15 ( 12-18 )
September	18 ( 15-22 )	56 ( 51-63 )	12 ( 10-15 )	14 ( 12-18 )
October	18 ( 16-23 )	50 ( 41-55 )	16 ( 13-19 )	16 ( 12-19 )
November	16 ( 12-20 )	54 ( 48-59 )	16 ( 12-20 )	14 ( 12-20 )
December	16 ( 11-20 )	54 ( 50-58 )	15 ( 10-19 )	15 ( 11-19 )

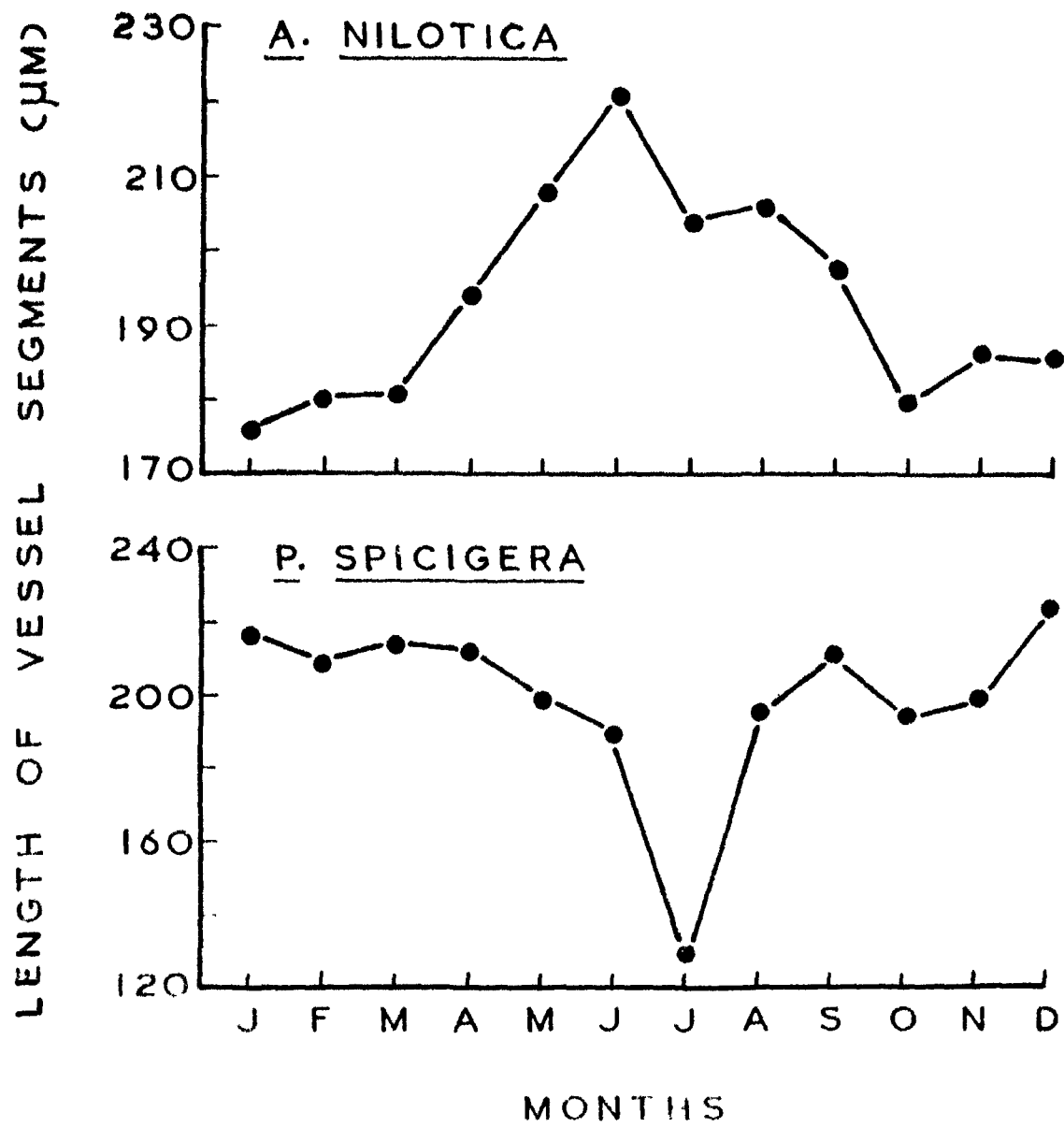


FIG. 16



TABLE 44

Seasonal variation in size of the vessel segments in Acacia nilotica. The average is based on 2400 independent readings. Values in parentheses indicate the range.

Months	Length ( $\mu$ m)	width ( $\mu$ m)
January	176.4 ( 90-260 )	30.6 ( 16-68 )
February	180.2 ( 90-260 )	43.2 ( 25-85 )
March	180.9 ( 60-245 )	41.6 ( 19-85 )
April	194.6 ( 60-265 )	29.8 ( 19-65 )
May	208.3 ( 90-295 )	45.0 ( 19-85 )
June	221.2 ( 90-380 )	48.5 ( 19-98 )
July	204.2 ( 90-328 )	42.9 ( 16-85 )
August	206.1 ( 60-300 )	51.7 ( 25-98 )
September	198.2 ( 60-310 )	41.2 ( 19-98 )
October	180.1 ( 60-245 )	38.4 ( 16-65 )
November	186.6 ( 60-260 )	36.9 ( 11-65 )
December	186.2 ( 90-260 )	38.2 ( 19-65 )

TABLE 45

Seasonal variation in size of the vessel segments in Protopia spicigera. The average is based on 2400 independent readings. Values in parentheses indicate the range.

Months	Length ( $\mu$ m)	Width ( $\mu$ m)
January	215.6 ( 17-300 )	136.7 ( 30-215 )
February	209.4 ( 75-310 )	128.9 ( 30-180 )
March	214.4 ( 45-285 )	121.4 ( 15-180 )
April	211.6 ( 45-300 )	98.6 ( 15-145 )
May	198.9 ( 45-270 )	114.0 ( 22-165 )
June	190.2 ( 45-270 )	134.5 ( 30-230 )
July	128.6 ( 30-225 )	124.9 ( 30-225 )
August	196.4 ( 45-270 )	124.0 ( 30-180 )
September	211.6 ( 30-270 )	127.4 ( 22-195 )
October	194.9 ( 45-290 )	128.1 ( 30-210 )
November	199.6 ( 30-265 )	156.3 ( 30-210 )
December	224.2 ( 75-300 )	153.8 ( 30-225 )

**TABLE 46**

Seasonal variation in size of xylem fibres in Acacia and Prosonia. The average is based on 4800 independent readings. Range in parentheses.

Months	<u>Acacia nilotica</u>		<u>Prosonia spicigera</u>	
	Fibre length (/um)	Fibre width (/um)	Fibre length (/um)	Fibre width (/um)
January	1124.2 ( 664-1328 )	16.6 ( 8-25 )	907.4 ( 480-1550 )	15.9 ( 12-29 )
February	1227.9 ( 913-1660 )	17.1 ( 10-30 )	1014.21 ( 480-1600 )	15.4 ( 12-22 )
March	1239.6 ( 1913-1826 )	17.4 ( 12-35 )	1010.4 ( 520-1600 )	15.0 ( 12-22 )
April	1187.3 ( 820-1660 )	15.8 ( 8-25 )	1073.1 ( 560-1680 )	16.0 ( 10-24 )
May	1216.1 ( 820-2000 )	16.7 ( 10-30 )	1090.0 ( 480-1680 )	16.9 ( 12-24 )
June	1211.3 ( 996-1826 )	17.6 ( 10-30 )	991.9 ( 480-1550 )	14.1 ( 8-20 )
July	1164.9 ( 664-1660 )	14.9 ( 8-22 )	1009.8 ( 520-1280 )	14.4 ( 12-20 )
August	1216.7 ( 664-1826 )	16.8 ( 10-24 )	970.2 ( 560-1290 )	13.8 ( 10-20 )
September	1321.6 ( 996-2000 )	17.8 ( 12-30 )	1012.5 ( 560-1312 )	15.2 ( 12-24 )
October	1150.4 ( 664-1660 )	16.1 ( 10-25 )	944.5 ( 480-1280 )	14.0 ( 8-22 )
November	1136.1 ( 584-1710 )	15.9 ( 10-22 )	985.6 ( 480-1556 )	13.9 ( 8-16 )
December	1090.2 ( 581-1660 )	14.6 ( 8-24 )	992.1 ( 520-1470 )	15.1 ( 8-22 )

## PERIODICITY OF CAMBIUM AND FORMATION OF SECONDARY TISSUES

Cambial activity: The vascular cambium in both the species experienced some definite periods of rest and activity during a calendar year. When dormant, the cambial region was represented by a narrow zone of tangentially flattened cells consisting in average of 10-17 layers in Acacia nilotica and 6-7 layers in Protonia spicigera ( Plates VIIA, VIIID ). Radial walls of these cells were comparatively thicker in dormant state than in the active one. In tangential view, the radial walls exhibited profound beaded appearance owing to the alternately thickened areas and the depressed primary pit fields through which plasmodesmata connections are established with the adjoining cells. Protoplasmic contents including nuclei were relatively dense and stained dark during dormancy ( Plate VIB & D ).

The first sign of reactivation of cambium was the appearance of "swelling" of the cambial cells which was followed by the onset of periclinal divisions and consequently the formation of secondary tissues. In the present study, "reactivation of cambium" applies to the initiation of periclinal division and not to the swelling of the initials. Time span between the appearance of swelling and the commencement of periclinal divisions is regarded as the "preparation

period". Prior to swelling, the nuclei of the cambial cells enlarged, and the protoplasmic content as a whole became light stained. Later the cells began to enlarge ( Plates VIIIB, VIIIA ).

In case of Acacia, such histochemical changes in the cambial cells were noted to take place around mid February, thus marking for the occurrence of swelling. Within a month the cells began to divide and the cambial zone which had an average of 10 cell layers, began to expand radially. Later, the width of cambial zone varied from 12 to 28 cells in average ( Plate VIIC & D ). The cell division remained in full swing by late October. It appeared to reach its zenith around September/October when the number of cambial cell layers went upto 36 at some places ( Table 47 ). During the active growth period, the radial walls of the cambial cells were stretched to be delicate enough to allow the detachment of bark from wood with even a slight pressure applied upon the bark. Also, the beaded appearance of the walls was not prominent, if at all ( Plate VIA ).

The rate of cell division declined during winter and the division ultimately ceased by January ( Plate VII A ). The cambial cells later on developed their dormant features such as dark contents, prominent beads, thickened radial walls, relatively smaller and darker nuclei etc. within a fortnight. The dormant period continued till the cambium

reactivated again in March ( Plate VII B ).

In a nutshell, the cambium in Acacia remained active from mid March till early January, showing thereby that the activity continued for about 9.5 months.

In Prosopis spicigera, on the other hand, the cambial population experienced the swelling phenomenon around mid March and the cell division started either in early April or at the end of March ( Plate VIII A & B ). It resulted in a slight expansion of the cambial zone. Prior to swelling, the cell content had cleared up and most of the cells took only a light stain. The cambial population went on growing and touched the vertex around July and August with a cambial zone consisting of about 17 cells layers ( Plate VIII C ). Average width of the cambial zone tended to decline a little during September and the radial growth came to a halt in October. On the whole, the average cell layers of cambial zone varied from 10 to 17 during the active phase of cambium.

From October onwards, the cambium underwent the period of rest showing all the cellular features associated with the dormant condition and continued to be so till the next growth period approached in March ( Plate VIII D ). This way, the cambium in Prosopis remained active for about 7 months, the remainder being the period of rest ( Table 47 ).

Time of initiation and cessation of the cambial activity did not exhibit any marked variation during the years of study i.e., 1975, 1976 and 1977. The "average cell layers in cambial zone" hitherto discussed represent the mean value of the readings obtained for all the three consecutive years.

Phloem/Xylem production: In Acacia nilotica, the conversion of the outer derivatives of cambium into new phloem elements started in April. It continued till late July and sometimes till August. Side by side, the initiation of xylem formation also set in around July. It gradually overcame the phloem formation which ultimately stopped by August, and continued as long as upto January. Thus, the time span of phloem and xylem formation extended over 5 and 6 months respectively ( Table 47 ).

In Prosonia spicigera also, the formation of phloem preceded that of xylem. At the advent of summer, after the resumption of cambial activity, the cambial derivatives began to differentiate into phloem elements. The phloem differentiation came to an end around June when the phenomenon switched over to xylem side. The xylem production commencing from July lasted till late in September or sometimes in October. Thus, the period of phloem and xylem differentiation in this species stretched over 3 and 4 months respectively ( Table 47 ).

TABLE 47

Seasonal activity of cambium and the formation of secondary tissues in Acacia and Prosonia. The average is based on 120 readings. Values in parentheses indicate the range.

Months	<u>Acacia nilotica</u>		<u>Prosonia spicigera</u>	
	Cambial layers	Differen- tiation	Cambial layers	Differen- tiation
January	17 ( 14-22 )	Xylem	6 ( 4-10 )	-
February	10 ( 6-12 )	-	6 ( 4-7 )	-
March	10 ( 7-14 )	-	7 ( 4-10 )	-
April	12 ( 7-15 )	Phloem	10 ( 6-12 )	Phloem
May	12 ( 8-15 )	Phloem	14 ( 9-18 )	Phloem
June	14 ( 8-15 )	Phloem	15 ( 12-18 )	Phloem
July	15 ( 10-17 )	Phloem & Xylem	17 ( 12-18 )	Xylem
August	20 ( 15-23 )	Phloem & Xylem	17 ( 12-20 )	Xylem
September	23 ( 18-26 )	Xylem	12 ( 9-16 )	Xylem
October	28 ( 24-36 )	Xylem	7 ( 5-10 )	Xylem
November	20 ( 16-23 )	Xylem	7 ( 5-12 )	-
December	20 ( 16-24 )	Xylem	6 ( 4-8 )	-



## RELATION BETWEEN PHENOLOGY AND GROWTH

Acacia nilotica var. telia was hardly ever quite leafless. New buds began to appear in February, at the advent of spring, and this continued as long as upto October-November. The old leaves had begun to fall before the new ones appeared and continued doing so while the young leaves were sprouting. The flowering season was somewhat irregular, mostly initiating in rainy season. The tree was noted to flower from May till December.

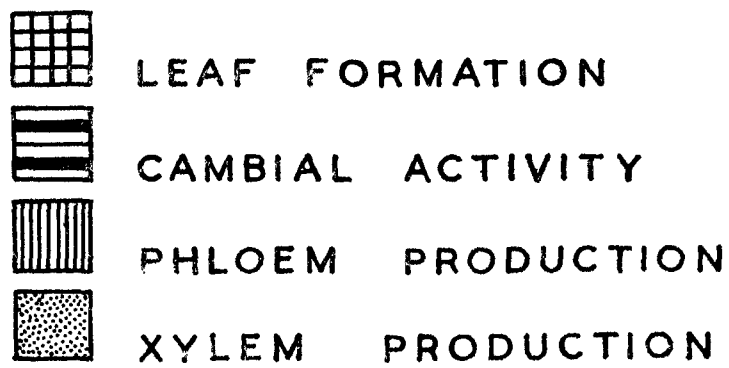
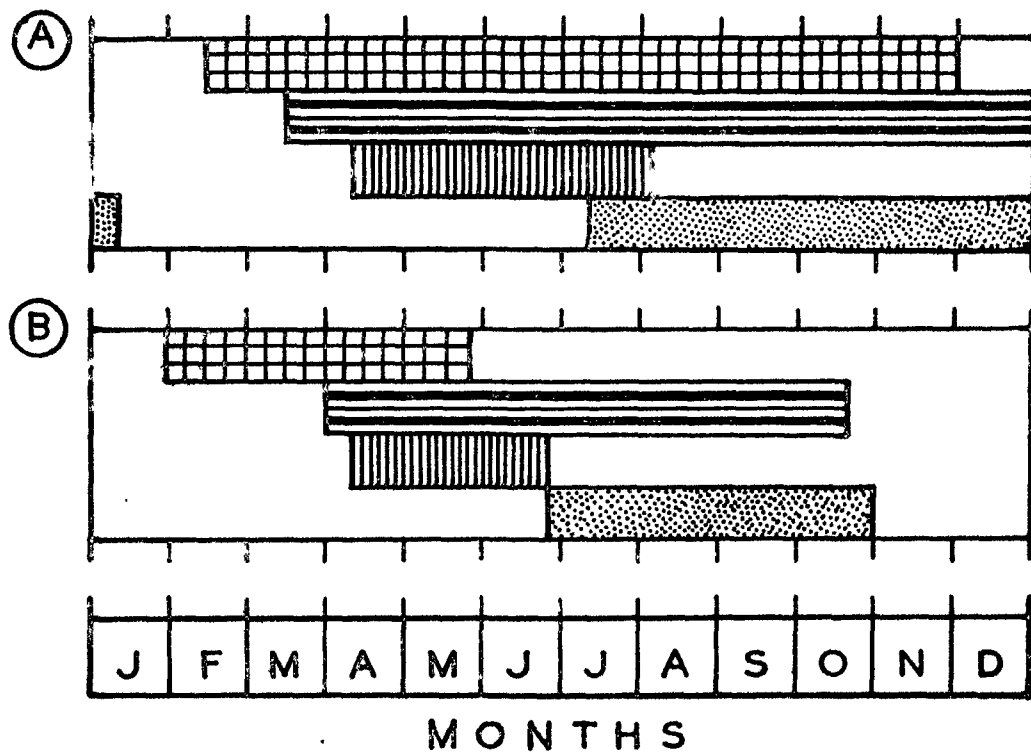
In Prosopis spicigera, the foliage became thin towards the end of cold season. Spikes of small yellow flowers appeared usually from March to May, after the formation of new leaves.

Both the selected trees viz., Acacia nilotica and Prosopis spicigera resumed their growth activity in late March when the temperature was about 25°C. The new leaf formation usually started in both the species in February with the air temperature ranging from about 10°C to 25°C during the years of study. Thus, the reactivation of cambium occurred after the resumption of the extension growth ( Fig. 17 ). In general, a moderately high temperature together with low humidity and long day conditions appeared to help in the reactivation of cambium. However, the

promotion of the cambial growth appeared to depend on relatively high temperature and high humidity in the atmosphere which prevailed during July-September after the break of monsoon rains in early July. At the advent of winter the fall of temperature in November-December eventually brought a stop to the cambial activity ( Table 47 ). The differentiation of the xylem elements was, however, noted to continue till January in the case of Acacia.

To sum up, the initiation of leaf emergence in Acacia preceded the swelling phenomenon by about a fortnight and the cambial cell division by about a month. In Prosonis, the leaf emergence preceded the swelling phenomenon by almost a month and the actual cell division by about 6 weeks.

# PERIODICITY OF CAMBIUM



A= A. NILOTICA  
 B= P. SPICIGERA

FIG. 17

## **D I S C U S S I O N**

## FORMATION AND STRUCTURE OF CAMBIUM

The term cambium was coined by Grew (1682), who believed it to be "a refined sap, which first coagulated and then assimilated with the wood". Knight (1807, 1808) considered that the bark and wood were derived out of fluid 'cambium'. Richard (cited by Trecul 1852) assumed the cambium to be an essential fluid in plants, like blood in animals, that nourished but did not get itself transformed into the growing tissue.

German authors were the first to recognize the cellular meristematic region and to apply the term cambium to them. Sanio (1863) differentiated the cambium from procambial tissue and restricted the term only to lateral meristems. Afterwards, de-Bary (1884) described the cambium to be a meristematic zone consisting of a single initial layer and the undifferentiated mother cells of phloem and xylem, a concept of cambium as conceived in general (cf. Raats 1892; Ladefoged 1952; Bannan 1955; Newman 1956; Wilson 1964; Fahn 1967; Kozlowski 1971; Philipson et al. 1971; Butterfield 1975; Ghouse & Iqbal 1979a).

It is commonly held that in dicotyledons, the cambium originates within the provascular strands and spreads tangentially to cover the interfascicular regions i.e., the

formation of fascicular cambium precedes that of inter-fascicular one (Esau 1965a). However, Fahn et al. (1972) have recently reported just the reverse in case of Ricinus communis. The observations in the present study, however, go in agreement with the commonly held view. The procambial cells were noted to experience periclinal divisions repeatedly in order to produce rows of radially aligned elements before they transformed into true cambial layers, as also noted by some earlier workers (cf. Esau 1938, 1942, 1943, 1965b; Gunckel & Wetmore 1946; Sterling 1946, 1947; Parke 1963; Cumbie 1967; Fahn et al. 1972; Ghose et al. 1972; Soh 1972, 1974a, b; Butterfield 1976). This made it rather difficult to recognize in transections the exact time of differentiation of the procambium into vascular cambium in the present study. However, taking the appearance of ray initials as a criterion (Cateson 1964), the cambial conversion is supposed in the present study to initiate first in the fascicular region.

The cambium, as in majority of vascular plants, was essentially made up of fusiform as well as ray initials in both the species studied, the arrangement of the initials depicting a typical non-stratified pattern. This type of cambium, found in most dicotyledons, gymnosperms and some arborescent fossil forms of pteridophytic level, is considered to be phylogenetically primitive (cf. Bailey 1923; Rames &

MacDaniels 1947; Metcalfe & Chalk 1950; Esau 1960, 1965a; Barghoorn 1964; Fahn 1974).

Bailey (1920b) measured the cambial initials of a large number of trees and found that fusiform initials were considerably shorter than the fibres and tracheids but more or less equal in size to vessel segments. Later, he concluded that the tracheids of gymnosperms and vessel segments of woody dicotyledons could possibly be used as indicators of the approximate length of fusiform cambial initials (Bailey 1923). The variation he found in length of fusiform initials of the different species ranged from 220-6800/ $\mu$ m among gymnosperms, from 170-410/ $\mu$ m and 460-4400/ $\mu$ m among the dicotyledons showing the storeyed and non-storeyed cambium respectively. The range of length (263-385/ $\mu$ m) obtained in the present study for fusiform initials, therefore, falls shorter than the one reported by Bailey (1923) for non-storeyed cambia. Instead, it is more closer to the Bailey's measurements for storeyed cambia. There is possibility that this shortness in the average cell length of fusiform initials in the species presently investigated might be indicative of their tendency towards phylogenetic advancement. The present findings, however, are not in much contrast from those recently obtained for a number of Indian tropical trees (cf. Ghouse & Yunus 1974a; Ghouse & Iqbal 1975; Ghouse et al.

1976a; Ghouse & Hashmi 1977a; Yunus et al. 1978 ).

It is known that the walls of fusiform cells, composed of the usual cellulose associated with non-cellulosic substances, have primary pit fields through which the communication with contiguous cells is established by means of plasmodesmata. Radial walls have been reported to be usually thicker than tangential walls especially during dormancy, and their primary pit fields appear deeply depressed (Eames & MacDaniels 1947; Evert 1963b; Esau 1965a; Mahmood 1968; Yunus 1976; Hashmi 1977). These features have been observed in the present study also.

The fusiform initials have been generally reported to be uninucleate regardless of variation in their size. Bailey (1920a) had demonstrated the uninucleate condition of fusiform cells of considerably large size in a number of gymnosperms. Recently, a multinucleate condition has been reported in fusiform cells of Delonix regia, Polyalthis longifolia and Mimusops elengi ( Hashmi 1977 ), Psidium guajava (Ghouse & Khan 1977) and Solanum melongena (Patel 1975). In the present study, the multinucleate condition has been found in one of the species (Acacia nilotica), the other one (Prosonia spicigera) usually showing uninucleate fusiform cambial cells. Unlike Ghouse & Khan (1977), no cognizable seasonal variation has been noticed in the nuclear status of



multinucleate fusiform cells of Acacia nilotica. The size and chromaticity of the nucleus have been reported to vary in different seasons, especially in dormant and active periods of radial growth (Derr & Evert 1967; Paliwal & Prasad 1970; Yunus 1976; Hashmi 1977). In the present study, the nuclei were observed to be relatively smaller in size and more darkly stained during the dormant period than in the active one.

The cambial initials undergo two types of division, anticlinal and periclinal (Bailey 1919). Anticlinal divisions result in the multiplication of cambial cells required to cope with the increasing circumference of the cambial cylinder due to radial growth. The phloem and xylem cells emanate from the periclinal divisions. Bailey (1923) recognized radial longitudinal and pseudotransverse divisions among the anticlinal type, the former being usually associated with stratified and the latter with non-stratified cambium. The radial longitudinal division occurs through the formation of a vertical cell plate from one end of the cell to the other in a radial plane, while the pseudotransverse one takes place with a cell plate running askew and intersecting the two radial walls at two different levels (Philipson & Ward 1965; Philipson et al. 1971).

Anticlinal divisions are generally restricted to the cambial initials in conifers and dicots (Cumbie 1967; Butterfield 1975) but they may be distributed over several

layers of cells in the cambial zone. The present study on Acacia and Prosopis also confirms the above. The anticlinal divisions, wherever noticed, were pseudotransverse with appreciably oblique dividing walls. Sometimes, the dividing walls were so long as to touch nearly the ends of the dividing cells. The dividing wall was usually laid down toward an end giving rise to daughter cells of unequal size.

The daughter cambial cells thus produced are believed to undergo apical elongation usually to attain the original size of mother cells. Krabbe (1886) postulated the theory of gliding or sliding growth suggesting that each cell in the meristem grows independently and the growth results in changes in position of the cell relative to one another leading to the formation of new cell contacts. Later, Priestley (1930) put forth his theory of symplastic growth for the elongation of cambial cells involving slow mutual adjustment of cell position with changes in cell size and shape. Sinnott & Bloch (1939) later suggested that the fusiform initials elongate by growth at tips only and proposed the term "intrusive growth". Tips of such growing cells are thin walled and rich in cytoplasmic accumulation. Apical growth of fusiform initials was also reported by Bannan (1956, 1968b), Bannan & Whalley (1950), Hejnowicz (1961), Zagorska-Marek (1975) and Hashmi (1977). In the present study too,

the daughter cells resulting from pseudotransverse divisions, have been found to elongate by their apices till they attain an adult state. Such a growth is often evidenced by certain apical manifestations of the growing cells such as forking or serration of the cell tips or their intrusion in the ray initial units etc.

The ray initials, forming an integral part of the cambium and occupying a considerable portion of its circumference, are present in most of the species. Origin and development of vascular rays have been ably described by Barghoorn (1940a, b, 1941a, b) and Braum (1955) in both conifers and dicotyledons. Some other pertinent studies include those of Klinken (1914), Beijer (1927), Chattaway (1933, 1938), Bannan (1941, 1950, 1951, 1953, 1956), Whalley (1950), Evert (1959, 1961), Cumbie (1963, 1967, 1969a, b), Srivastava (1963a, b), Cheadle & Esau (1964), Ghouse & Yunus (1973), Ghouse & Iqbal (1977a) and Khan (1977).

Barghoorn (1940b) classified the vascular rays as primary and secondary depending on their origin. He further found that the structurally primitive dicotyledons possessed both uniseriate and multiseriate rays. The uniseriate rays in primitive forms were tall and composed of vertically elongated large cells while the multiseriate ones had a

main body made up of nearly isodiametric cells and long wings consisting of similar to those of uniseriate rays. In the present study, both of the species analysed have a composition of uniseriate as well as multiseriate rays, but the multiseriate ones do not possess such uniseriate wings. They, however, consist of cells of uneven size. Their height and width may go to the extent of 100 cells and 9 cells respectively.

Various ways of ray development have been described by earlier workers. A single cell may be cut at the end of a fusiform cell which may act as a ray initial; a declining fusiform initial may be reduced to a single ray initial; part of a fusiform cell or whole of it may be segmented by transverse divisions to form a tier of potential ray initials; or a lateral cell may be cut off the side of a fusiform cell to form a ray initial (for review, Philipson & Ward 1965, Philipson et al. 1971). In Acacia and Prosopis studied presently, all the above types of ray initial formation have been observed. However, the segmentation of fusiform cells was relatively less abundant. Further multiplication of the so formed ray initials and also the fusion of closer ray units gave rise to the tall and broad rays. Concomitantly, splitting of long and broad rays into smaller

ones has also been noticed frequently in both the species studied. Similar observations were made in various species by earlier workers (cf. Barghoorn 1940a, b; Esau 1965a; Evert 1961; Cheadle & Esau 1964; Ghouse & Yunus 1973; Hashmi 1977; Khan 1977 ). The split of rays is brought about chiefly by the intrusion of fusiform initials into a panel of ray initials and also by the conversion of ray initials into fusiform initials (Chattaway 1933, 1938; Barghoorn 1940b; Bannan 1941, 1950; Evert 1961). On the other hand, conversion of intervening fusiform initials into a row of ray initials also results in the formation of long ray initial units in the species investigated. Similar reports on the fusion of ray initial units have appeared for a number of species (cf. Barghoorn 1941b; Braun 1955; Evert 1961, 1963b; Ghouse & Yunus 1973).

As to the relative proportion of the two types of initials, Bailey (1923) noted that fusiform cells occupied approximately seven-eighths of the total circumference of cambial cylinder in Pinus, a much less proportion in many dicotyledons and a little less than one half in certain extreme cases. Wilson (1963) calculated the surface area of cambial zone occupied by fusiform initials to be more than 90% in Abies concolor. Based on this, he also proposed a model for the cambium of conifers ( Wilson 1964). Kozlowski (1971) also voted for a similar composition of cambium in

general. Studies of Butterfield (1972) on Aeschynomene hispid have brought out that fusiform cells may constitute even more than 95% of the cambial zone in certain angiosperms.

Contrary to the above, Ghouse & Yunus (1974a, b, 1976a), Ghouse & Iqbal (1976), Ghouse et al. (1976a), Ghouse & Hashmi (1977a), Yunus et al. (1978) and Ghouse & Jamal (1979) made it clear that the fusiform cells may not necessarily constitute as high a proportion as reported earlier. They found that in the majority of Indian tropical trees screened by them, the proportion of fusiform cells varied from 60-85% but in certain extreme cases, the proportion might fall as low as only 25% (Ghouse & Yunus 1974b). They also found the proportion of cambial initials to vary considerably in trees of different age-groups (Ghouse & Yunus 1973; Ghouse & Iqbal 1977a). Recently Margaris & Papadogianni (1977) have worked out the relative proportion of cambial initials in plants belonging to the 'maquis' and 'phrygana' types of plant communities (Eyre 1968) growing in mediterranean region. They have noted the average proportion of fusiform initials to be 83% in maquis and 92% in phryganic species, thus substantiating the earlier conclusions emanated from the work in both the temperate and tropical regions.

In the present study, the average proportion of fusiform initials did not exceed 86% in both of the species.

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The observations are, therefore, at par with the earlier ones on other tropical trees of India referred to above.

## STRUCTURE OF DERIVATIVE TISSUES

The phloem of Acacia and Prosopis is clearly divisible into conducting and non-conducting zones. The conducting part with intact sieve-tube elements gradually converts into the non-conducting one when the sieve-tube members are obliterated or crushed due to the ever increasing stress from inner derivatives or when the companion cells lose their protoplasts. Sieve-tube members in both the species are generally long, slender and enucleate bearing distinct sieve-areas on their lateral walls and the compound sieve-plates on noticeably inclined or oblique end walls. They are arranged in non-stratified fashion, as do their mother cambial initials. These features indicate the evolutionary status of the species under investigation.

The sieve-tube members were found more or less comparable in length with fusiform initials of their respective cambium. Apical intrusive growth was also encountered in some of the sieve-tube members, though the number of such elements was extremely rare. Occurrence of intrusive growth in sieve-tube members has been reported by Ghouse & Yunus (1975) in some Dalbergia species. Such a growth was, however, denied by Cheadle & Esau (1964) in their ontogenetic study of secondary phloem of Liriodendron tulipifera.



Sieve-tube cells are known to translocate the photosynthate ever since their discovery by Hartig (1837). In early thirties, it was estimated by Crafts (1931, 1933) that only 17% and 23% of the phloem in cucurbit stem and potato stolon respectively was engaged in the translocation process. In other words, only this much portion of the phloem was occupied by sieve-tube members. He, therefore, concluded that  $1/5$  of the phloem takes part in mass-transfer phenomenon. The figure was noted to be  $2/3$  in some tree trunks by Munch (1930, 1941). Lawton & Canny (1970) and Canny (1973) pleaded for the Munch's value ( $2/3$ ) to utilize in calculations of specific mass-transfer studies. Later works (Lawton 1972, 1976; Grange & Peel 1975; Ghouse & Hashmi 1976; Ghouse et al. 1976b; Ghouse & Iqbal 1978) have, however, elucidated the need of an independent estimation of the mass transfer medium for each species individually, as a prelude to physiological studies pertaining to translocation. The present study has revealed that the amount of sieve-tube members hovers around  $1/2$  and  $1/5$  of the conducting phloem in Acacia nilotica and Prosopis spicigera respectively. Thus, the phloic composition of one of the species confirms the Craft's assumption while that of the other tends to plead for Munch's conclusion. The vast difference of the two values, however, urges to accept the recommendation of the earlier workers for making a

separate analysis of the phloem of each species under study.

Phloem sclerenchyma, the mechanical tissue of the bark, form the next important constituent of the phloem; their distribution being a characteristic feature worthy of attention for systematic purposes (Holdheide 1951; Zahur 1959; Santos 1960; Ghouse et al. 1979). Recently, attempts have been made to exploit the distribution pattern and relative amount of phloem sclerenchyma in the identification of isolated bark materials of some related genera and species ( see Ghouse & Yunus 1974c; Ghouse & Jamal 1978; Ghouse et al 1979 ).

Phloem fibres which form a major part of the sclerenchyma, are mostly narrow, elongated elements with long tapering ends and lignified walls. Most of the fibres in Acacia were noted to be septate as was found in Vitis ( Strasburger 1891; Esau 1948 ) and Dalbergia ( Ghouse & Yunus 1975 ), but in Prosopis they were generally non-septate. They were considerably longer than the fusiform initials ( about 4 times in Acacia and 6 times in Prosopis ) they had originated from. This is apparently due to the apical intrusive growth which seems to be universal among phloem fibres of the species investigated, as reported for certain other tropical trees of India ( see Ghouse & Sabir 1974; Ghouse & Yunus 1975; Siddiqui et al. 1976; Ghouse & Iqbal 1979b ). The intrusively grown fibre tips exhibited several morphological and histochemical modifications

such as broad lumen, apical forking, serration and dentation etc., presence of cytoplasm and negativity to some specific stains showing the absence of lignification. Similar observations were made by Liese & Parameswaran (1972) as well as by Ghouse and his co-workers (cited above ).

The direction of intrusive elongation may be polar. In Thuja occidentalis, elongation of the cambial cells was found to be considerably greater in the downward rather than in the upward direction (Bannan 1956). On the contrary, the upper ends of the ramie fibres (Boehmeria nivea) continued to grow for a longer period than did the basal ones (Kundu & Sen 1961). A recent investigation (Wenham & Kusick 1975) has demonstrated the lack of uniformity in the polarity as well as in the amount of elongation of wood fibres even if they are derived from the same cambial initial. One may elongate more upwards while the other downwards. The polarity could not be determined in the present study because of the elements being studied in macerated form.

The present investigation more or less conforms to earlier ones which showed the apical elongation of fibres to range from 3 to 7 times the length of the mother initials e.g. in Cannabis and Corchorus (Kundu 1942) and in some Dalbergia species ( Ghouse & Yunus 1975 ). It also supports the idea of intrusive growth of the phloem fibres to be of common occurrence, in tropical trees at least.

On the other side, the wood of both Acacia and Prosopis is diffuse porous. The vessels are usually isolated from one another or sometimes occurring in radial multiples of 2-3 or more. Their relative proportion in mature tree trunk was noted to vary from 12-34% in Acacia and 16-32% in Prosopis. Fibres formed the major portion of wood in both the species. Unlike sieve-tube members in the phloem, the vessel segments were invariably shorter in length than the mother fusiform initials. Similar results were obtained by Khan (1977) for Psidium guajava and by Anand et al. (1978) for Dalbergia sissoo. The xylem fibres, having shown evidences of intrusive growth, were shorter in length than phloem fibres in the species investigated. The reverse has been reported by Anand et al. (1978) who found the wood fibres in Dalbergia to be 8-9 times while the phloem fibres to be 6.2 times longer than fusiform initials.

#### EFFECT OF AGE ON CAMBIUM AND ITS DERIVATIVES

It is almost an established fact that the average size of cambial initials varies with their position in the tree axis. Earlier studies indicate that the length of fusiform initials increases with the increasing age of the meristem, but after reaching certain maximum, it usually remains relatively stable ( Bailey 1923; Carlquist 1962; Ghose & Yunus 1973 ). The length of fusiform initials in Acacia was found to follow similar trend, although there was a fall in length in a sample which was obtained from the basal part of the tree trunk and, therefore, contained the oldest meristem. It might be due to the proximity of root system. In case of Prosopis, the fusiform cell length increased with the age of cambium but the correlation reversed after the length had attained the maximum, resulting in a gradual but slow decline in length with further increase in the girth of stem axis or, in other words, in the age of the meristem. Thus, the findings do not agree with those authors who described a constant rather than a decreasing length of fusiform initials after the attainment of the maximal size ( Bailey 1923; Carlquist 1962; Ghose & Yunus 1973 ), an overall increase in length throughout ( Cumbie 1969a), or

an early stabilization after an initial increase ( Bailey 1944; Carlquist 1962; Cumbie 1963, 1967, 1969b; Butterfield 1972 ).

The length of fusiform initials is believed to be related partly to the frequency of pseudotransverse divisions and partly to the loss of the initials. The former tends to depress the cell length, while the latter enhances the elongation of adjoining cells ( Philipson et al. 1971 ). The short fusiform initials recorded in the present study in younger stem axes may, therefore, be attributed to the probable abundance of pseudotransverse divisions in such portions as reported by Wilson (1966) in the case of Pinus strobus. The decline in length of the initials at the basal part of the trunk (with the most senile cambial cylinder) seems to be attributable to the "exhausted" condition of the meristem itself due to its old age rather than to the frequency of pseudotransverse divisions, as the cambial cylinder does not expand here as vigorously as in the younger branches. According to Chouse & Iqbal (1977a), it appears that after passing a certain age limit the initials gradually lose their capacity and vigour for apical elongation, as also evident from the measurements of their tapering ends. Significance of apical elongation in partly determining the

length of the corresponding initials was also speculated upon by Ghouse & Yunus (1974b). It will be interesting to mention here that Bannan (1961, 1964) inferred from his data on conifers that the high frequencies of pseudotransverse division do not depress the cell length as much as it might be expected, because the rapid elongation associated with the high frequencies of divisions, and the continuous elimination of the shortest fusiform initials mitigate the effect of the division. He concluded that the cell size variation was due to inherent determiners rather than to the rate of anticlinal division. Similarly, Echols (1955, 1958) emphasized upon the significance of inherited characters in determining the consistent pattern of length variation in tracheids of certain Pinus species.

It has been enunciated by earlier workers ( Sanio 1872; Bailey & Shepard 1915; Lee & Smith 1916; Chalk 1930; Bethel 1941; Dadswell & Wardrop 1949 ) that in a certain growth ring the mean length of fusiform initials increases from the base upwards reaching a maximum at about one-third of the stem height and then decreases towards the top. It can be pointed out that the maximum length of fusiform initials in Prosonia spicigera is also found somewhere around 1/3 of the stem height. In Acacia nilotica, however, the longest initials are relatively closer to the base.

The present observations reveal that the ray initials do not undergo any appreciable change in their individual dimensions in relation to the increasing girth or the relative age of the axis. They, however, increase in number and form the broader ray initial units in older axes. The same has been noted in certain other species by Bailey (1923), Braum (1955), Ghouse & Yunus (1973), Ghouse & Iqbal (1977a), Hashmi (1977) and Khan (1977). However, Gregory (1977) observed that in Acer saccharum ray initials increased in size as they aged, slowly when growth rate was slow, rapidly when it was high, but there was little fluctuation in the number of rays per unit of tangential area.

Ratio of ray and fusiform initials also differs in the cambium of different age. The proportion of fusiform initials in Dalbergia sissoo was found to decrease with the growing age of cambium by Ghouse & Yunus (1973). Similar is the case with Acacia nilotica as worked out in the present study. The fusiform cells constitute about 71 to 86% of the total tangential area of cambial cylinder as revealed by screening the cambium at different levels of the tree axis. In Prosonia spicigera, the ratio of fusiform initials amounts to 67 to 85%. Although the proportion is relatively high in younger axes than in older ones, no regular and systematic variation trend was observed all along the axis.



Influence of the age of the mother meristem has also been detected in secondary tissues. An almost gradual increase in bark thickness vis-a-vis age of the axis was noted for Delonix regia, Polyalthis longifolia, Mimusops elengi (Hashmi 1977) and Psidium guajava (Khan 1977). The present study brings out a similar case of Prosopis spicigera. In case of Acacia, however, the bark thickness becomes more or less constant in the adult tree trunk. This agrees with the observations of Yunus (1976) on Dalbergia sissoo.

It was noted by Anderson (1951) for the wood of certain conifers that the cell length at any given distance from the central core was constant throughout the trunk, irrespective of the number of growth rings involved. Hejnowicz & H<sup>j</sup>nowicz (1958) also obtained similar observations for a 50 year old tree of Populus tremula and concluded that the distance from the central pith was a comparative measure of the number of cambial generations involved in the wood formation and hence, of the relative age of cambium. This means the elements situated at the same distance from the central pith at various heights of the axis were formed by the cambium of the same age. Thus, the length of fusiform initials and their derivative cells is more closely related to the relative rather than the absolute age of the cambium measured in terms

of growth rings. Xylem elements have been studied with respect to the age of the plant or the girth of stem axis by a pretty large number of workers (see Spurr & Hyvarinen 1954; Dinwoodie 1961) and most of them have endorsed the Sanio's generalizations for cell size variation (see Sanio 1872). Phloem elements, however, are yet to be screened extensively with a view to find out their response to age.

In order to find out the ontogenetic changes or the ageing effect on the cambial derivatives, comparison should be made among those elements which are differentiated at diverse distances from the central pith in different growth rings. Now from the pith outwards, the pattern of cellular variations is apparently greatly affected by growth conditions prevailing in the different growth years. The best information, therefore, can be had from the study of such elements which are differentiated in the same growth year but at the different girth and height levels of the axis because such elements, in spite of occurring at considerably varied distances from the central core, are produced under the same environmental factors and growth conditions.

The present study carried out with all these considerations reveals that in case of phloem, the various component elements especially the fibres and sieve-tube members undergo

considerable proportional and dimensional changes in relation to the tree age in Acacia and Prosopis. Relative proportion of sieve-tube members was noted to be greater in younger axes than in older ones.

The fibres were non-existent or very scanty in the conducting phloem of younger axes. When the fibres were fully differentiated, their proportion was found to decrease in Acacia and to increase in Prosopis in relation to the growing axis girth. Further the length of sieve-tube members showed a gradual increase from the top of the tree downwards in both the species. Phloem fibres, always present in the secondary phloem as a whole, experienced an initial increase in length which soon came across a reversal when the length began to decline with further increase in girth or decrease in height of the stem axis.

On wood side, the proportion of vessel segments did not show any regular variation pattern in Acacia and remained almost stable after a slight increase in upper portion of the trunk in Prosopis. With certain deviations, their length had a gradual gain with the increasing axis girth and after having reached a maximum, it stayed almost constant in Acacia and declined slightly in Prosopis with further radial growth. Proportion of wood fibres, on the other hand, varied in a decreasing order in Acacia while in an increasing order

in Prosonia with growing girth or, in other words, with increasing age of the stem. Mean length of the fibres, however, did not evince any significant trend of variation.

In all the variation trends mentioned above, the last sample of the material collected from the basal part of the trunks, usually posed a deviation from the normal trends observed. This might be due to the probable influence of the root system developed nearby, as was speculated by Hejnowicz and Hejnowicz (1958) in Populus tremula and by Purkayastha et al. (1974) in Michelia champaca, while working on the cell dimension of wood elements.

Recently Pattanath (1972) and Purkayastha et al. (1974) have worked out the fibre length variation in relation to the height of stem in some bamboos and Michelia champaca respectively. The length tended to be greater in the basal portion than at the higher levels, showing no systematic variation trends. Iqbal & Ghouse (1977a), while describing the ontogenetic size variation of vessel elements in Prosonia spicigera, have pointed out that the length and width of vessel elements increase and the angle of end wall inclination (deviation from vertical plane) decreases with increasing girth of stem axis, whereas the number of pits per unit area of the vessel walls remains almost constant after an initial decrease in upper parts of the axis.

The length of fibres and vessel elements, at any level in the tree axis of Ulmus procera, was noted to increase from pith outwards through a number of growth rings until it reached certain maximal value, beyond which the cell elongation ceased. Final size of the elements in a specific growth ring increased from the bottom topwards, reached a maximum at a definite height, and then decreased further towards the top (Sundrasivarao et al. 1973). These elements, in Aesculus hippocastanum, showed an initial rapid increase in length at any one level of the axis which was gradually nearer than higher up the base. In a specific ring, the elements increased in length upto a certain height (Sundrasivarao & Nazma 1977). Datta et al. (1976) have found that the length of axial wood parenchyma, like the pore-diameter and ray-width, increases with the girth of trunks in Strychnos nux-vomica. The present study, however, remains from demonstrating any significant and systematic dimensional change in axial parenchyma.

Moreover, it should be germane to emphasize here that the marked variation in transectional area of sieve-tube members and vessel segments at different levels of stem axis also urges not to use any fixed value of the translocation pathway, no matter if it is Craft's  $1/5$  or Munch's  $2/3$  value, for the estimation of mass transfer phenomenon throughout

the stem, but to find out independent values of the available pathway even for different parts of the same individual (cf. Iqbal & Ghouse 1977b, 1979).

At a particular level of the tree axis, the length of sieve-tube members was noted to decrease with respect to their position progressing from the cambial region towards the periphery in both the species analyzed presently. Angle of inclination of the sieve-tube end walls also decreased accordingly. This seems to reflect the combined effect of the size of mother cambial initials and the intrusive growth which the sieve-tube elements experienced after differentiation. The former is thus responsible for the decrease in length while the latter for that in end-wall inclination of the elements. Occurrence of intrusive growth in the phloem of these species has been reported recently (Ghouse & Iqbal 1979b). Since the sieve-tube elements undergo only a slight intrusive growth and that too usually in the form of apical tails (Ghouse & Yunus 1975), their main body does not elongate markedly and hence, the size of these elements is closely related to that of the precursor cells. However, since a good many factors including size of fusiform initials, degree of intrusive growth, development of parenchyma along with the sieve elements, and the prevailing internal

conditions influence the size of sieve-tube members (Esau & Cheadle 1955), the variation pattern is not strictly regular but beset with occasional fluctuations. Similar observations on sieve-tube length variation have been made by Liese & Parameswaran (1972), Ghouse & Yunus (1976b) and Ghouse & Iqbal (1977b).

The phloem fibres, on the other hand, were noted to experience an initial decrease near cambium, subsequently followed by a gradual increase toward the periphery in Acacia nilotica. On the contrary, an initial gain in length followed by an ultimate decline at the periphery was noted for the fibres in Prosopis spicigera. Obviously, the shorter length of fibres found in the outer bark regions is attributable to some extent to the shorter length of the younger cambial initials from which they had developed, albeit the fibre length probably depends more on the degree of intrusive growth the elements have experienced than on the length of their precursors. In cases where the fibres are longer in peripheral region than near the cambium, intrusive growth seems to have played a decisive role and the elements appear to have experienced either a relatively rapid or a long lasting apical elongation. The various vicissitudes encountered in the length variation pattern across the bark

might be owing to changes in growth during the different growth years. These observations revealing a cognizable trend of cell length variation are at par with some earlier reports on certain tropical species (Liese & Parameswaran 1972; Parameswaran & Liese 1974; Ghouse & Siddiqui 1976a, b; Ghouse & Yunus 1976b; Ghouse & Hashmi 1977b; Ghouse & Iqbal 1977b; Yunus et al. 1977).

Similar observations on the wood elements of these species revealed that xylem fibres increased in length more or less gradually from the centre outwards but had a decline in the vicinity of cambial cylinder. This is in conformity with a number of earlier studies (for review, Spurr & Hyvarinen 1954; Dinwoodie 1961). Vessel segments showed a somewhat irregular length variation. However, the segments near the central core were mostly smaller than those near the cambium.



SEASONAL VARIATION IN THE STRUCTURE OF  
CAMBIUM AND ITS DERIVATIVE TISSUES

Earlier studies have revealed that the structure of vascular cambium as well as of the derivative tissues does not remain stable all the year round. Instead, their component elements undergo proportional as well as dimensional changes in relation to the varying seasonal conditions. Paliwal & Prasad (1970, 1971) and Paliwal et al. (1975) tried to demonstrate some positive correlations between the cambial activity and fusiform cell size in case of Dalbergia sissoo and Polyalthia longifolia respectively. In case of Dalbergia the minimum cell size was found before the commencement of the growth period. The size increased with the onset of cambial activity, attained a maximum after the activity had reached its zenith, and then declined toward the end of the growth period, all with certain occasional irregularities. More or less similar results were obtained for Polyalthia. Yunus (1976) and Hashmi (1977), however, did not find any consistent correlation between the cell size and cambial growth in both the above species respectively.

In the present study, the fusiform initials increased almost consistently as the activity enhanced in Acacia. There was a sharp decline around August-September, the period of

wood formation, after which the length regained its previous range of magnitude during winters. In Prosonia, the length showed a slight increase with the onset of cambial activity. It, however, dropped slightly during July when the wood formation set in. The length later slumped a great deal around September, i.e., at the end of the growth period. The sudden fall in length recorded in both the species might be due to the onset of anticlinal divisions at that particular time. Such reports are not uncommon in the relevant literature (cf. Bannan 1950).

Abundance of the ray initial units of different widths and heights as well as the relative proportion of the two types of initials has also shown considerable variation with changing season. In Acacia, the multiseriate rays which are most frequent throughout the year showed a relatively meagre proportion at the onset of cambial activity. It reached its vertex, on the other hand, during the grand growth period. The tetraseriate units, second in the relative abundance, showed just an opposite variation trend. In case of Prosonia, no regular pattern was found for the variation in relative abundance of the different types of rays in relation to season. Similar was the case with the rays of varying height in both the species.

Consequent to the variations in cambial construction, the proportion of ray and fusiform initials also kept fluctuating. The latter, however, never exceeded an average value of 85%. Some similar observations have been recorded by Yunus (1976), Hashmi (1977) and Khan (1977) with certain other tropical trees in India.

Further, the average thickness of conducting phloem was noted to vary from 1.3 to 2.3 mm in Acacia and from 0.5 to 1.1 mm in Prosopis. Thus, the former case conforms to the findings of Evert (1962) in Tilia americana and of Hashmi (1977) in Polyalthia longifolia and Mimusops elengi. The latter, on the other hand supports the findings of Holdheide (1951) on some temperate zone trees and consequently substantiates the general view that the conducting phloem usually forms less than a millimeter in depth ( Easu 1965a ). Whitmore (1962), however, assumed the conducting phloem to be 5-6 mm thick in Dipterocarpaceae. Evert (1960, 1963a, b), Lawton & Lawton (1971), Lawton (1972, 1976), Yunus (1976) and Khan (1977) have also studied the seasonal variations in the secondary phloem of some tropical trees.

As regards the size variation of sieve-tube members, it is found that their length varies from about 245 to 324/ $\mu$ m in Acacia and from 282 to 311/ $\mu$ m in Prosopis in a calendar year. In both the species the elements were generally longer in the

later part of a year than around the early growth season.

According to Esau (1965a), sieve-tube elements occupy from 25 to 50% of the area of conducting phloem. However, their proportion was found to vary from 17 to 57% at different times in a year in the species investigated by Lawton (1972). In the present study, the sieve-tube proportion did not exceed 59 and 41% during a year in Acacia and Prosonia respectively.

Khan (1977) recognized 3 types of vessel elements (narrow, medium and large) in Psidium guajava but there was no particular sequence in their occurrence. The author did not detect any cognizable seasonal effect on the wood structure in this diffuse-porous species. In the present investigation, it was noted in Acacia that the proportion of vessels was higher from July till October than during the rest of the year, the minimum being noticed from April till June as well as in December. Besides, the average vessel element length which measured from about 176 to 221  $\mu$ m during the different months, was deemed to slump slightly during winter and to increase during summer. In case of Prosonia, the maximum amount of vessel segments was noted during March to April. They were relatively longer during winter and spring.

PERIODICITY OF CAMBIUM AND PRODUCTION  
OF SECONDARY TISSUES

Barring a few exceptions in tropical species (Alvim 1964; Pahn 1974), the majority of dicotyledons exhibit a periodic rather than continuous radial growth. The continuous growth of certain tropical species is attributed to the favourable climatic conditions which prevail more or less the whole year around equatorial zone. The growth in tropics, if not continuous throughout the year in most of the species, is more prolonged than in temperate conditions where the growth period is relatively short and hardly exceeds 4-5 months. Studies of Chowdhury (1940, 1968, 1969) on the cambial activity of some Indian tropical trees have revealed certain examples of as long a span of radial growth as 10 months. Similar studies by Pahn & Barnat (1963), Hao (1972), Lawton (1972), Chou & Chiang (1973), Pahn (1974), Lu & Chiang (1975), Chiang (1976), Yunus (1976) and Khan (1977) have also shown the cambium to remain active either for a major part of the year or throughout the year. However, Paliwal & Prasad (1970) and Paliwal et al. (1975) have shown the growth period in Dalbergia sissoo and Polyalthia longifolia respectively to be as short as in some temperate species. The present study elucidates that the cambial activity goes for about 8 months

in Acacia nilotica and about 7 months in Prosopis spicigera. It is in agreement with the earlier observations on other tropical species such as Acacia raddiana (Fahn 1967), Cedrela toona (Chowdhury 1968), Eucalyptus gigantea (Amos et al. 1950), E. camaldulensis (Fahn 1967), Tamarix aphylla (Fahn 1967) in which the cambium has been found to be active for about 8-10 months. In some other species like Acacia cyanophylla, A. tortilis and Tamarix articulata (Fahn 1974), the cambial activity is reported to continue throughout the year.

In all the three years of this study, the cambial reactivation took place only after the new leaf formation. Together with the onset of cambial cell division, a decrease in the density of cell protoplast, in the thickness of cell wall, in the beaded appearance of radial walls of fusiform initials and in the amount of tanniferous contents in ray cells was also recorded. This goes parallel to the earlier studies of Derr & Evert (1967), Tucker & Evert (1969), Paliwal & Prasad (1970), Paliwal et al. (1975), Yunus (1976), Hashmi (1977) and Khan (1977). Cambial reactivation has been noticed here in the present study in March. Cessation of the activity approached around late October to mid-November. Thus, the observations pertaining to the cessation of cambial activity conform to those of Chowdhury (1968), Yunus (1976) and Hashmi (1977) on a number of Indian tropical trees, while those

concerning the initiation of the activity are sufficiently different. In majority of cases dealt by Chowdhury (1968) and Hashmi (1977), the cambium became active around May and June.

As regards the production of secondary tissues, it was found that the formation of phloem preceded that of xylem in both species of the present investigation. A similar condition has been reported in Acer pseudoplatanus (Cockerham 1930), A. platanoides (Huber 1939), A. negundo (Tucker & Evert 1969), Pinus banksiana, P. resinosa and P. strobus (Alfieri & Evert 1968), Populus tremuloides (Davis & Evert 1968), Pyrus communis (Evert 1960), P. malus (Evert 1963b), and Vitis venifera (Esau 1948). Recent observations of this condition include those of Lawton (1972) on certain Nigerian forest trees, of Chiang (1976) and Lu & Chiang (1975) on two Taiwanese species and of Yunus (1976) and Hashmi (1977) on some Indian tropical trees.

In case of Acacia, the phloem production was noted to start in April and continue upto August. The xylem, on the other hand, started differentiating in July and this continued upto January. Thus, a simultaneous production of both the tissues occurred during July and August. In case of Prosopis, the phloem formation was noticed from March till June followed by the xylem formation which lasted from July till

October. Contrary to the findings of Strasburger (1891), Brown (1915), Abbe & Crafts (1939), Wilcox et al. (1956), Grillo & Smith (1959), Srivastava & O'Brien (1966) and Tucker & Evert (1969) in various species, no partially differentiated over-wintering precursor phloem was found in the present study. This is, on the other hand, in support of the observations made with Acer spp. (Cockerham 1930; Elliott 1935; Huber 1939) and Pinus strobus (Alfieri & Evert 1968 ).

The derivatives on either side undergo differentiation, as usual, through cell expansion, cell division, wall thickening and lignification in both the species. The amount of cell expansion happens to be the greatest in sieve-tube members and vessel segments and the least in fibres. The ray cells expand only slightly and do not show any remarkable change during differentiation as it was reported by Kozlowski (1971). A large number of phloem cells remain thin walled and eventually collapse or become greatly distorted. The sieve-tube members develop usual nacreous wall while the fibres have distinctly thick secondary walls.

It is evident from the present study that the cambial activity is not only influenced by the prevailing weather conditions of the plant habitat but also by some physiological



factors such as bud bursting, leaf initiation and leaf fall. As to the environmental factors controlling the cambial activity, the effect of temperature can be taken to be most important to some species such as Robinia pseudacacia (Waisel & Fahn 1965), Dalbergia sissoo (Paliwal & Prasad 1970; Yunus 1976), Polyalthis longifolia (Paliwal et al. 1975; Hashmi 1977; Ghose & Hashmi 1979), Liquidambar formosana (Lu & Chiang 1975) and Isoetes taiwanensis (Chiang 1976). But in desert regions, the amount of available water in the soil becomes important. In certain plants, e.g. Acacia raddiana, A. tortilis and Tamarix articulata which grow in the deserts of Israel, the cambium is active throughout the year because their roots reach the levels that contain a certain amount of moisture even at the end of dry summer (Fahn 1958a, b). A similar situation has been found in Acacia caven growing in Chile (Aljaro et al. 1972). Sometimes the cambial activity coincides with the rainfall as in the case of Proustia cuneifolia (Aljaro et al. 1972) and Zygophyllum dumosum (Waisel et al. 1970). In addition to these factors, the endogenous growth rhythm may persist in spite of the influence of external factors. For instance, Eucalyptus camaldulensis indigenous to Australia, keeps its annual rhythm of cambial activity even when grown in Israel (Fahn 1959 ).

Paliwal & Prasad (1970) and Paliwal et al. (1975) inferred from their studies on Dalbergia sissoo and Polvalthia longifolia that the high temperature, high humidity and short day conditions are required for the initiation of cambial activity. They noted the activity in Dalbergia to cease in August when the temperature as well as relative humidity was considerably higher (30°C and 61% respectively) than that in February (15°C), the time of cambial reactivation. The temperature in August was only 5-6°C less than that prevailing in May when the activity was noted to reach its zenith (Paliwal & Prasad 1970). This was later criticized by Yunus (1976) who found the cambium of the same species to be active in March (Temp. 25°C, R.H. 55%). The activity was maximum in August (30°C, 79%) and came to a halt in late November (20°C, 56%). Further, Paliwal et al. (1975) denied any direct correlation between new leaf formation and the initiation of cambial activity in Polvalthia. Later, Hashmi (1977) and Ghouse & Hashmi (1979) were able to recognize a relationship between the bud emergence and unfolding of new leaves with the initiation of cambial activity in this as well as some other species. They also clarified that neither a high humidity nor short day condition, but a moderately high temperature (28-32°C) was essential for the cambial reactivation. However, a high temperature and a heavy rainfall

followed by high humidity was noted to promote rather than to initiate the cambial activity.

It was shown by Chou & Chiang (1973) that in Psidium guajava, the active period prolonged from February till November. The activity showed a positive correlation with temperature but it slowed down as the average temperature exceeded 28°C in July. The flowering period and the cambial activity exhibited a little correlation. Interestingly, Khan (1977) found the cambium in Psidium guajava to undergo activation twice a year after having experienced definite periods of rest. He tried to correlate this phenomenon with the peculiar habit of the tree to flower and fruit twice a year. The first sign of activity was noted in March and that of dormancy in May. Reactivation of cambium again took place in late July and the dormancy reapproached in October, the total period of cambial activity, including the temporary dormant phase, thus came to be about 8 months in this plant (Khan 1977). According to Chou & Chiang (1973), the cambial activity had initiated before the bud-burst, but Khan (1977) observed that the extension growth always preceded the radial growth in this species. It should be, however, pointed out that the observations of the former workers were based on sections from young branches, while those of the latter, on sections from the main trunk of the guava tree.

In the present study, the radial growth has been found to follow the extension growth and a close relationship between the new leaf formation and the onset of cambial activity is recognized. The gap between the leaf emergence and cambial reactivation was relatively longer in Prosopis than in Acacia. It might be due to the fact that in this species the flowering occurred immediately after the initiation of new leaf formation and the small amount of growth hormones produced by the young leaves might have been consumed in the beginning by the developing flowers.

Thus, the present observations conform to those of Coster (1927-28), Chowdhury (1939, 1957, 1968), Chowdhury & Tandon (1950), Paliwal & Prasad (1970), Yunus (1976), Hashmi (1977), Khan (1977) and Ghouse & Hashmi (1979) who have shown a direct bearing of the bud-bursting and new leaf formation on the initiation of cambial activity.

## **C O N C L U S I O N S**

The present study on the structure and activity of vascular cambium and on the formation and variation of its derivative tissues in the stem of Acacia nilotica and Prosopis spicigera has led to the following conclusions:

1. The vascular cambium develops first in fascicular regions and later extends to interfascicular ones to form a complete ring in both the species.
2. The cambium consists of two types of cells viz. fusiform initials and ray initials. The latter are usually grouped together to form 'ray initial units' of diverse shape and size.
3. The arrangement of cambial initials results in a non-stratified type of cambium in both the species.
4. Fusiform initials are uninucleate in Prosopis and mostly multinucleate in Acacia.
5. After pseudo-transverse division the newly formed initials which are generally unequal in size, grow intrusively to become as long as or even longer than the mother fusiform initial.
6. Mean length of fusiform initials in Acacia stem increases with increasing width of the trunk but after reaching certain maximum it declines slightly. This post-maturity decline is rather more prominent in Prosopis.

7. The over all increase in the length of fusiform initials does not exceed 75% and 40% of their initial length found in the first year shoot of Acacia and Prosopis respectively.
8. Ray initials, homogeneous in both the species, undergo greater multiplication to increase their number as the trunk grows older and wider.
9. New ray initial arises either from an apical cell cut at the end of fusiform initial or as a lateral cell cut off the side and occasionally by transverse segmentation of a whole or part of the fusiform initial.
10. Relative abundance of ray initial units of diverse width and height varies with growing girth of stem axis and the percentage of broader units is comparatively more in older trunks.
11. Relative proportion of fusiform and ray initials also varies with the axis girth. The formers constitute more of the cambial zone in younger shoots than in older trunk.
12. Mean length of fusiform initials in adult tree trunks undergoes variation in different seasons. The cells are comparatively shorter in April and then in August-September in Acacia stem. Their length increases from

February till June, suffers a decline further till September and then again increases during winters in case of Prosopis.

13. Multiseriate ray initial units are most abundant in Acacia throughout the year while in Prosopis their number remains quite meagre. Instead, tetraseriate units are dominant in this case.
14. Relative proportion of fusiform initials in Acacia tends to be greater during the grand growth period. No regular variation trend is discernible in case of Prosopis.
15. The bark, divisible into zones of conducting phloem, non-conducting phloem and rhytidome, increases in thickness with the growing axis girth but the bark-wood ratio which is 1:2 and 1:3 in young shoots of Acacia and Prosopis becomes 1:11 and 1:26 respectively in the main trunks.
16. Of the phloem elements, sieve-tube members possess compound sieve plates on their noticeably inclined or oblique end walls in both the species. Phloem fibres are mostly septate in Acacia and aseptate in Prosopis. Their distribution pattern is diagnostic in both the species.



17. Both sieve-tube members and fibres experience intrusive growth, mostly monopolar in sieve members and bipolar in fibres. The fibres grow about 3.6 times the length of mother initials.
18. Sieve-tube members constitute about  $2/5 - 2/3$  and  $1/5 - 2/3$  of the conducting phloem all along the stem axis of Acacia and Prosopis respectively. They occupy more area in younger stems than in older ones.
19. Mean length of sieve-tube members increases continuously in relation to age or the girth of Acacia stem, while it becomes more or less constant after attaining certain maximum in old tree trunks of Prosopis.
20. Mean width of the sieve-tube members also varies more or less corresponding to the length variation trend although the measurement differences are not so sharp in this case.
21. Length variation of sieve-tube members is not very gradual and systematic in relation to season. However, the length remains somewhat suppressed during early months of a calendar year in the case of Acacia.
22. Phloem fibres may not differentiate in the conducting phloem of young shoots. When differentiated, their proportion may either decrease (Acacia) or increase (Prosopis) with increasing girth of the axis.

23. From the top of the tree downwards, the length of phloem fibres initially increases with increasing axis girth. After attaining the maximal value, it begins to decrease with further increase of the trunk width in both the species.
24. The fibre length tends to decline during June to September as compared with the rest of the year. The variation pattern is, however, not so consistent and systematic.
25. The amount of axial parenchyma is more in younger axes than in older ones. Reverse is the case with phloem rays.
26. Relative proportion of the different phloic elements differs slightly with change in season but no systematic variation pattern is usually recognized.
27. On the wood side, vessel segments initially gain in the relative proportion from the tree-top basewards which later becomes constant along the older axis in Prosonia. No cognizable variation trend is found in Acacia.
28. With certain vicissitudes, the mean length of vessel segments increases with respect to the axis girth till it reaches certain maximum. With further increase in the axis girth, it becomes more or less constant in Acacia and suffers an ultimate decline in Prosonia.

29. The mean width of the vessels changes irregularly with respect to season or tree age in Acacia. In Prosonia, it gains an ultimate increase in the older axis and the variation is irregular in relation to season.
30. The length of vessel segments in Acacia remains somewhat retarded during winter (October-March) and tends to increase during summer (April-September). Conversely, the vessel length in Prosonia is usually greater during winter and early spring (December-April).
31. Relative proportion of vessels in the sap wood of Acacia tends to be appreciably higher during late summer (July-October) while in Prosonia it is so during early summer (March-May). On the contrary the proportion of fibres is relatively less during these periods as compared with that in other months.
32. The wood fibre proportion declines almost regularly with increasing axis girth in Acacia while it increases gradually in Prosonia.
33. Mean length of wood fibres in Acacia gradually increases in upper parts of the stem axis and later becomes somewhat irregular in the trunk region. In Prosonia, the initial increase undergoes slight fluctuations and ultimately attains a constancy in basal part of the trunk.

34. Mean length of the fibres does not exhibit any cognizable and consistent trend of variation in relation to season.
35. Reactivation of cambium takes place at different times in the species investigated. Swelling phenomenon occurs in Acacia and Prosopis trunks around mid-February and mid-March respectively.
36. Cell division initiates within 2-4 weeks after the swelling, and the cambial zone attains a maximum width around September-October in Acacia and around July-August in Prosopis.
37. The cell division stops by the end of December in Acacia and late in October in Prosopis. Differentiation of xylem, however, continues till January and early November respectively.
38. The cambium remains active for about 9.5 months in Acacia and about 7 months in Prosopis. Production of phloem precedes that of xylem in both the species.
39. A moderately high temperature seems to be inductive for cambial reactivation. Combined with high humidity, it promotes cell division in the cambial zone. Once initiated, the cambial activity appears to be capable to continue even at relatively lower temperatures.

40. Emergence of new leaves precedes the cambial reactivation in both the species. A considerable gap between the new leaf formation and cambial activity in Prosopis may be because of the probable consumption of the initial amounts of auxin produced by the young leaves in the flowering phenomenon which immediately follows the leaf emergence in this species.

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\* Not seen in original.

**P H O T O - P L A T E S**

**PLATE - I. Vascular cambium and conducting phloem  
of Acacia nilotica:**

- (A) T.L.S. of cambium showing ray and fusiform initials; (x150)
- (B) T.L.S. of phloem showing sieve tube members (ST) and other associated elements. Arrows indicate the oblique, compound sieve plates; (x225)
- (C) T.S. of phloem. Arrows indicate the fibre fascicles; (x150)
- (D) Magnified view of a portion of (C). Arrows indicate companion cells. (x600)

**F.I. = Fusiform initials**

**P. = Parenchyma (axial)**

**P.F. = Phloem fibres**

**R. = Rays; Ray initials**

**S.T. = Sieve-tube members.**

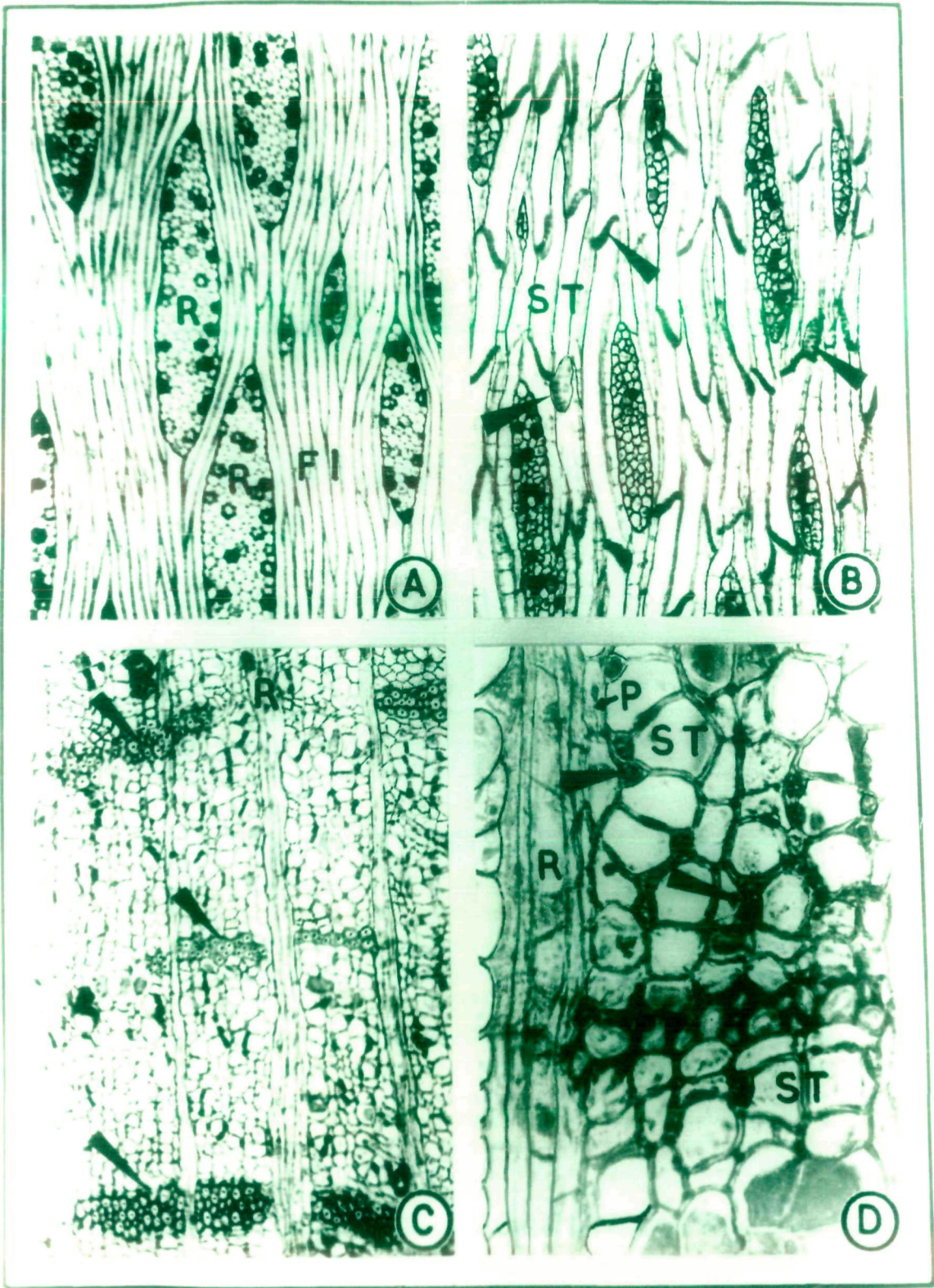


PLATE I

PLATE - II. Vascular cambium and conducting phloem of  
Prosopis spicigera:

- (A) T.L.S. of cambium showing ray and fusiform initials. ( x 150 )
- (B) T.L.S. of phloem. Arrows indicate the sieve plates. ( x 225 )
- (C) T.S. of phloem. Arrow indicates the phloem ray. ( x 150 )
- (D) Magnified view of a portion of (C). Arrows indicate companion cells. ( x 600 )

F.I. = Fusiform initials

P. = Parenchyma (axial)

P.F. = Phloem fibres

R. = Rays; Ray initials

S.T. = Sieve-tube members.



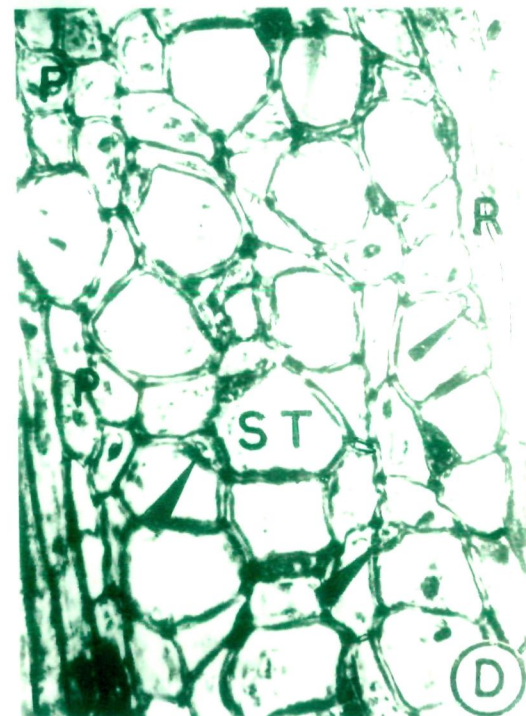
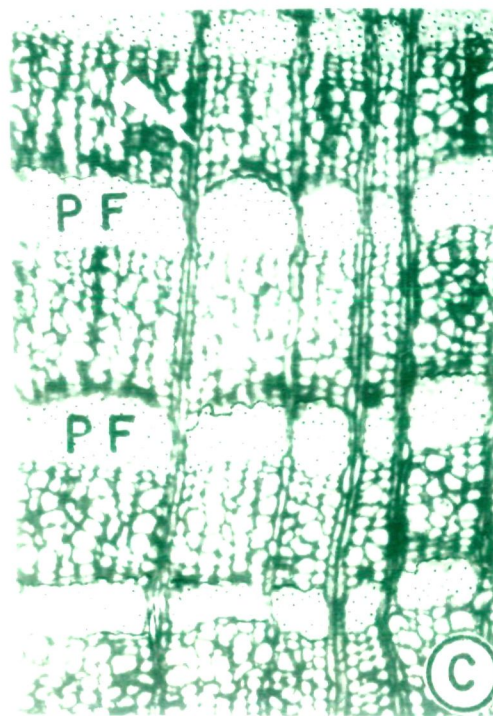
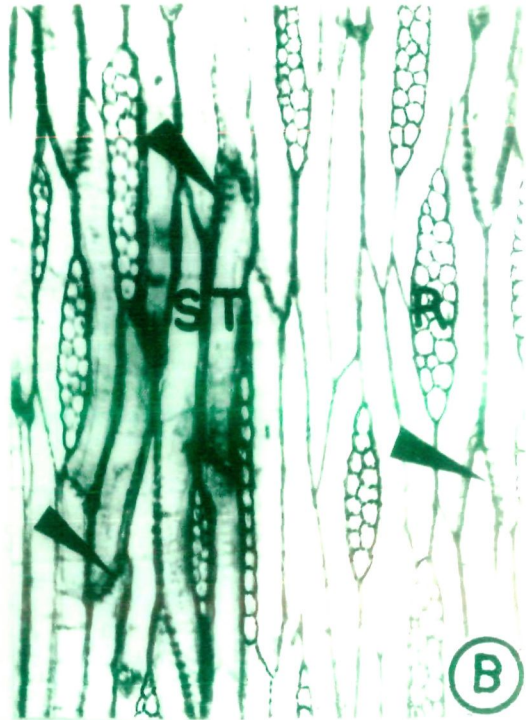


PLATE II

PLATE - III. Formation of ray initials in Acacia nilotica  
as seen in tangential views

- (A) Ray initial cut at the end of fusiform initial (arrow)
- (B) Transformation of a large apical portion of fusiform initial into a row of ray initials (arrow)
- (C) Multiplication of the ray initials developed at the end of a fusiform cell (arrow)
- (D) Thinning of a fusiform initial bearing a ray initial unit at its end (arrow), due to the lateral expansion of neighbouring fusiform cells.
- (E) Formation of ray initials from lateral side of fusiform initial (arrow)
- (F) A biseriate lateral ray initial unit.

Multinucleate condition of fusiform initials  
can be seen in different figures ( All  
at x600 ).



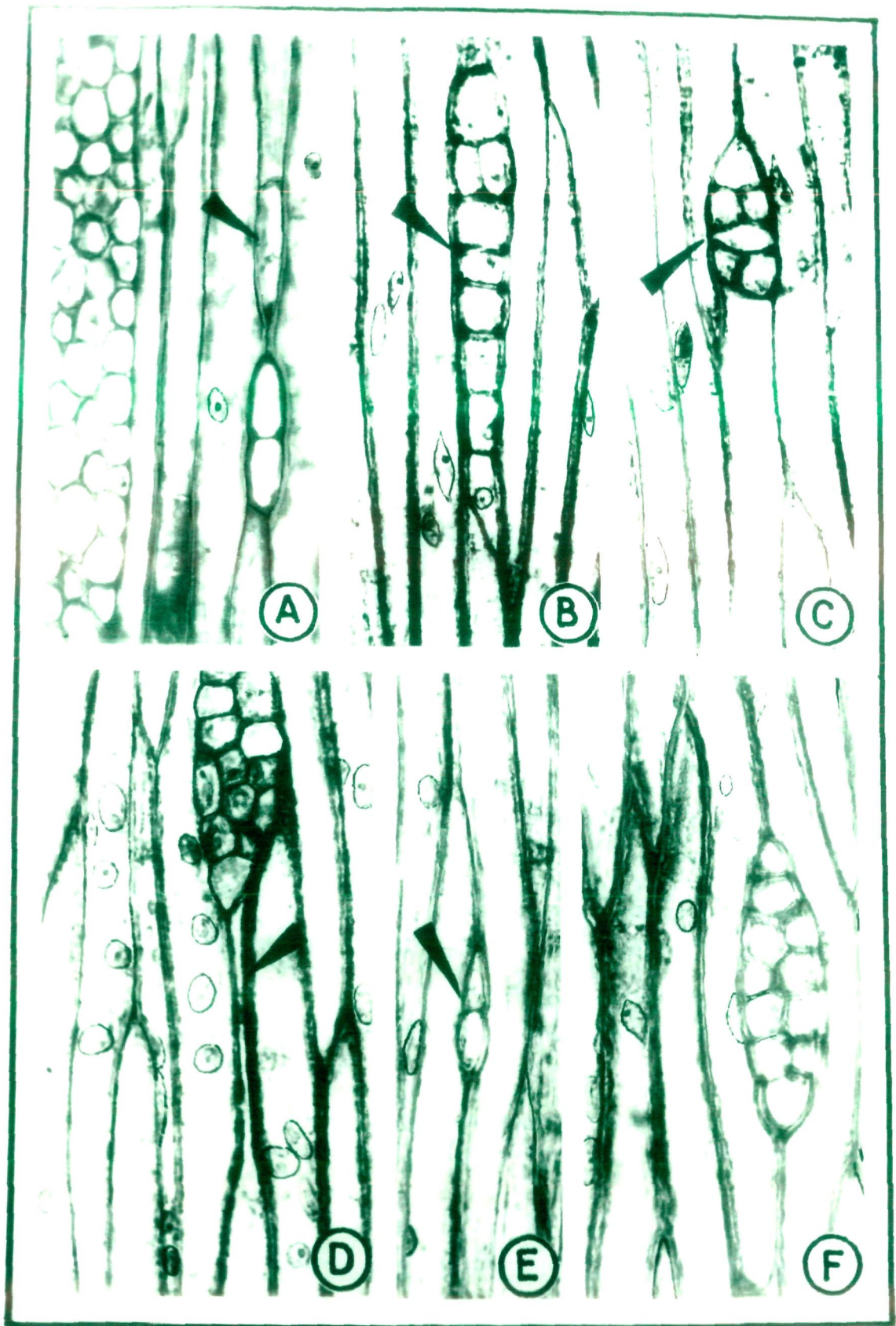


PLATE III



PLATE - IV. Transformations in the cambium of Acacia  
nilotica as seen in tangential view:

- (A) Formation of ray initials at the opposite ends of two contiguous fusiform initials (arrow).
- (B) Fusion of two ray initial units by their ends (arrow).
- (C) Segmentation of a fusiform initial (arrow) adjacent to a uniseriate ray initial unit lying at its left.
- (D) Segmentation of a fusiform initial (arrow) splitting a broad pannel of ray initials.
- (E-F) Apical growth of fusiform initials (arrows)

Multinucleate condition of fusiform initials  
can be seen ( All at x600 ).

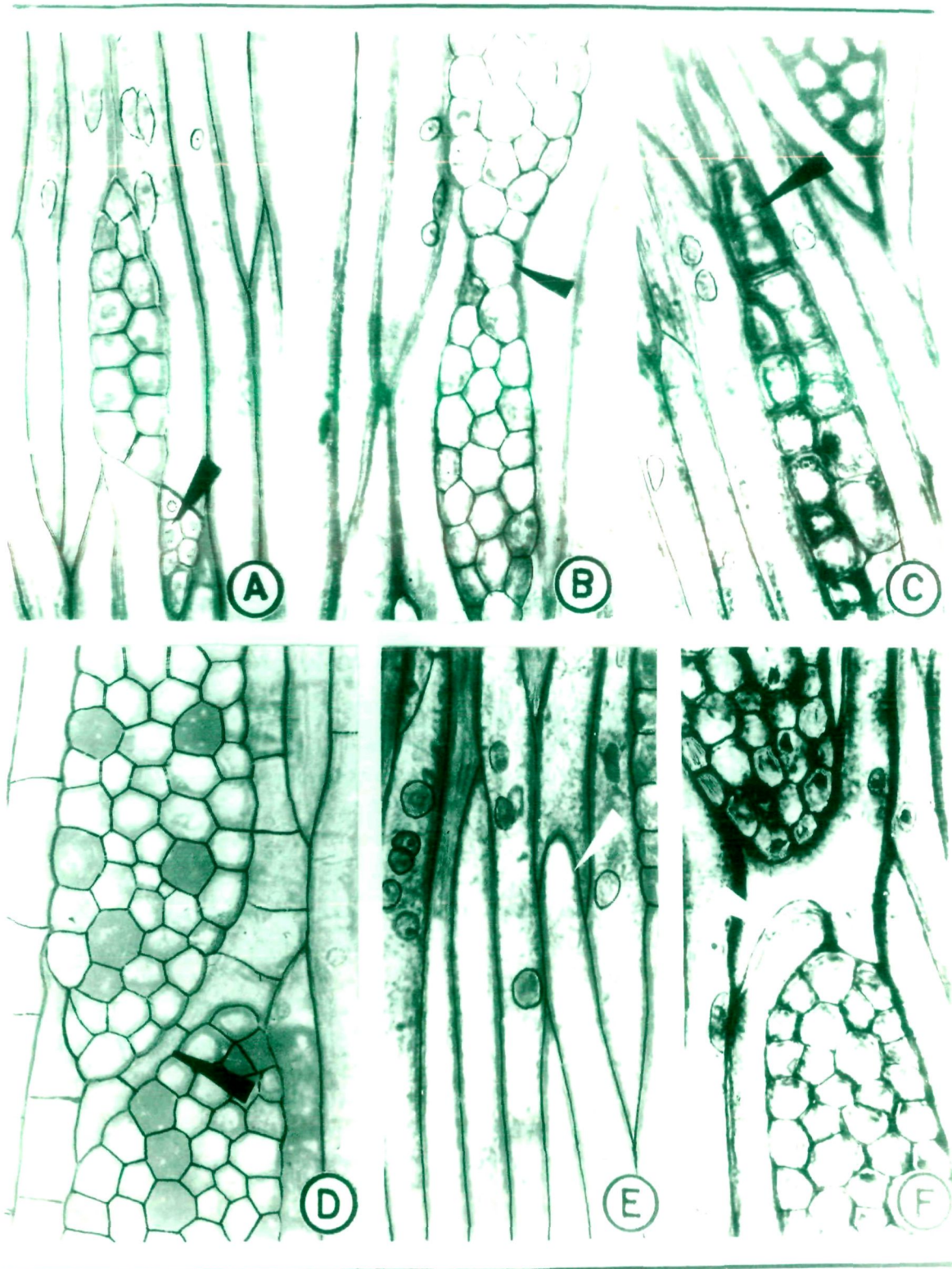


PLATE IV

PLATE - V. Splitting of ray initial units in Prosopis  
spicigera as seen in tangential views

- (A-C) Apical intrusion of fusiform initials (arrows) into broad pannels of ray initials.
- (D) Development of fusiform cell (arrow) out of ray initials in a broad ray-initial unit through their fusion and elongation.

( All at x600 )

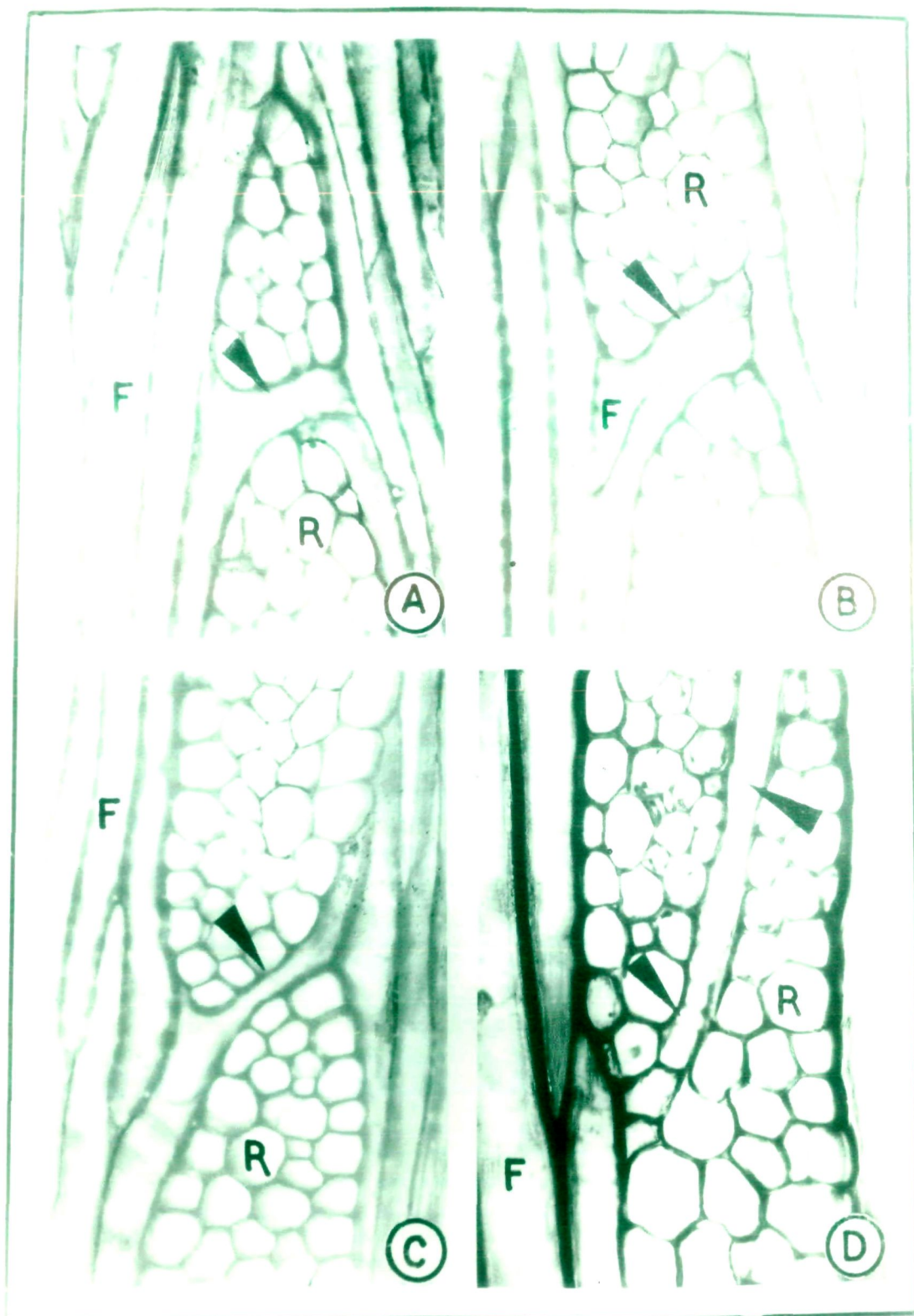


PLATE V



PLATE - VI. Cambium of Acacia nilotica and Prosopis  
spicigera in active and dormant states as  
seen in tangential view:

- (A) Cambium of A. nilotica in active state with the cambial initials having relatively thinner walls, clear cytoplasm and light stained nuclei.
- (B) Cambium of A. nilotica in dormant state exhibiting thicker cell walls with prominent beaded appearance (arrow), dense cytoplasm and dark stained nuclei.
- (C) Cambium of P. spicigera in active state showing all the characteristic features as in (A).
- (D) Cambium of P. spicigera in dormant state with all characteristic features as in (B).

A, B & D belong to the main tree trunk  
whereas C to a relatively younger axis.  
(All at x600).

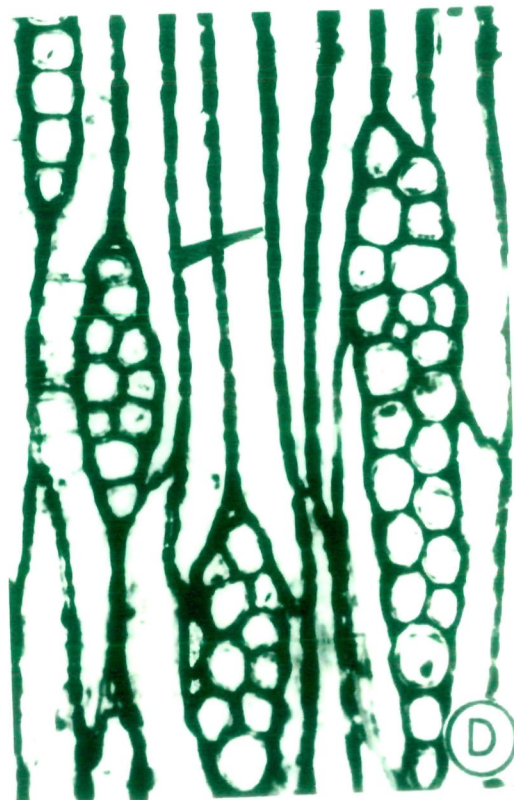
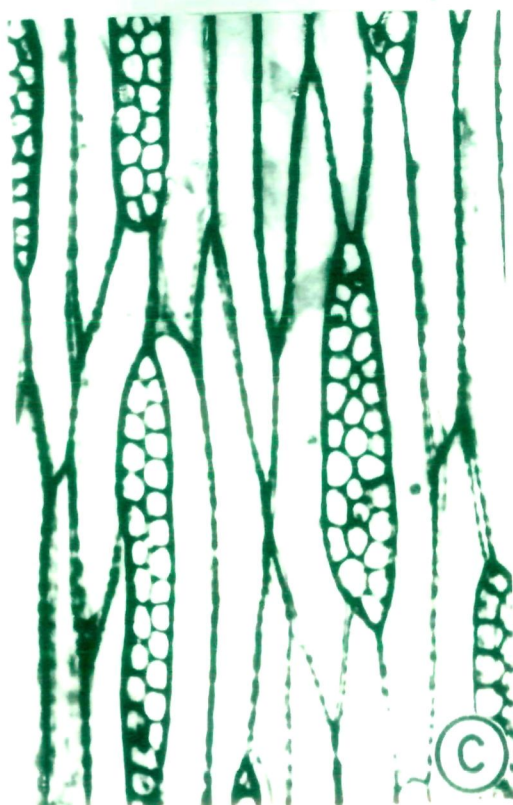
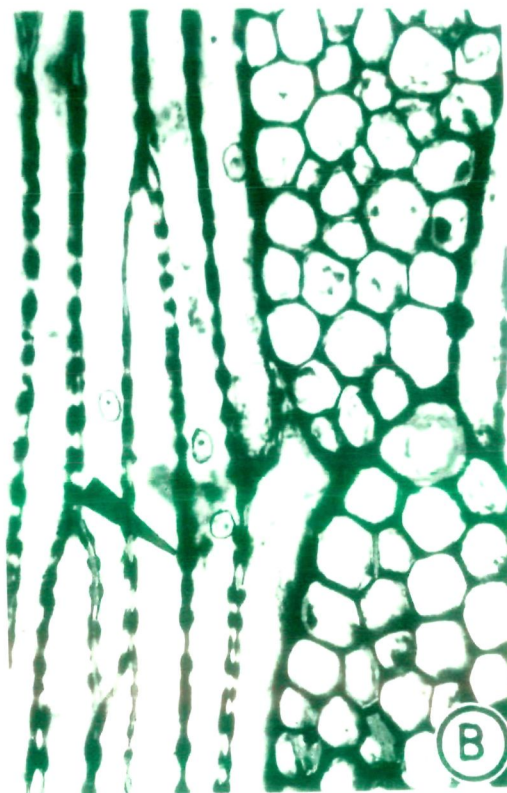
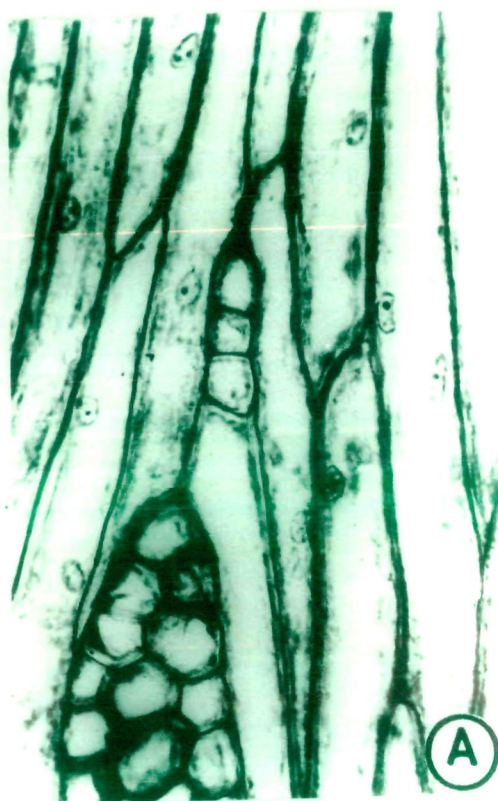


PLATE VI

PLATE - VII. Periodicity of cambium in Acacia nilotica  
as determined from transverse sections:

- (A) Cambium in January showing narrow cambial zone flanked on both sides with mature elements of derivative tissues.
- (B) Cambium in March showing the swelling (arrow) as well as division of cambial cells.
- (C-D) Cambium in August and September showing broader cambial zones.

Vertical bars indicate the width of cambial zone. Phloem on the upper side, xylem on the lower side of cambium.

( All at x600 ).



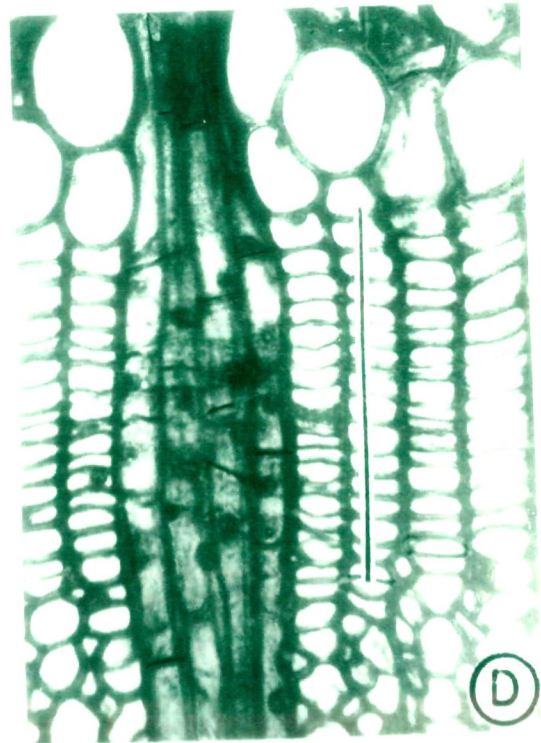
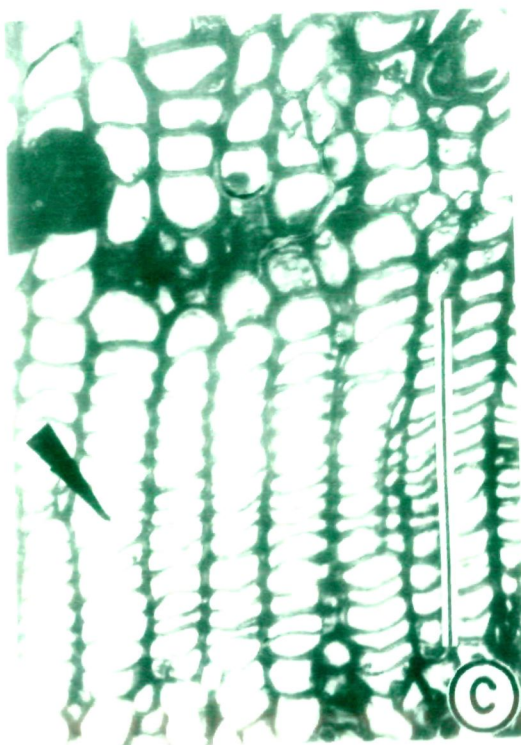
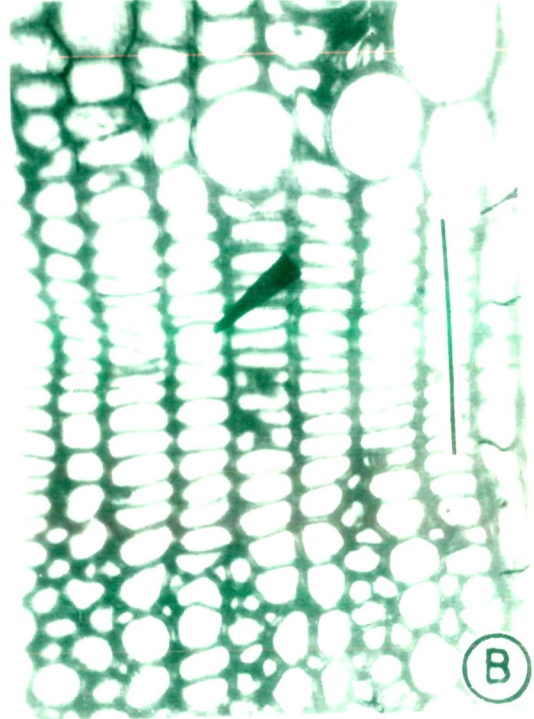
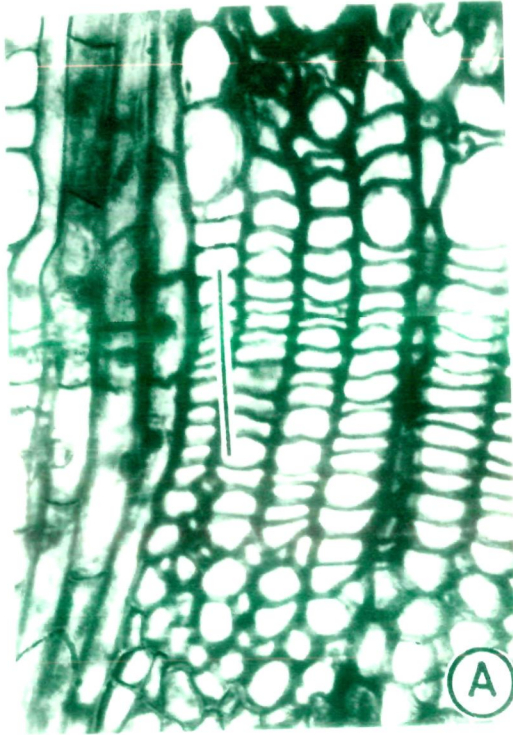


PLATE VII



PLATE - VIII. Periodicity of cambium in Prosopis spicigera  
as determined from transverse sections:

- (A) Cambium in March with relatively thicker cell walls and narrower cambial zone. Clearing of cells has started.
- (B) Cambium in April when the cells have started dividing (arrow).
- (C) Cambium in August showing a broad zone with dividing cells (arrow).
- (D) Cambium in December when dormancy has approached.

Vertical bars indicate the width of cambial zone. Phloem on the upper side, xylem on the lower one.

( All at x600 ).

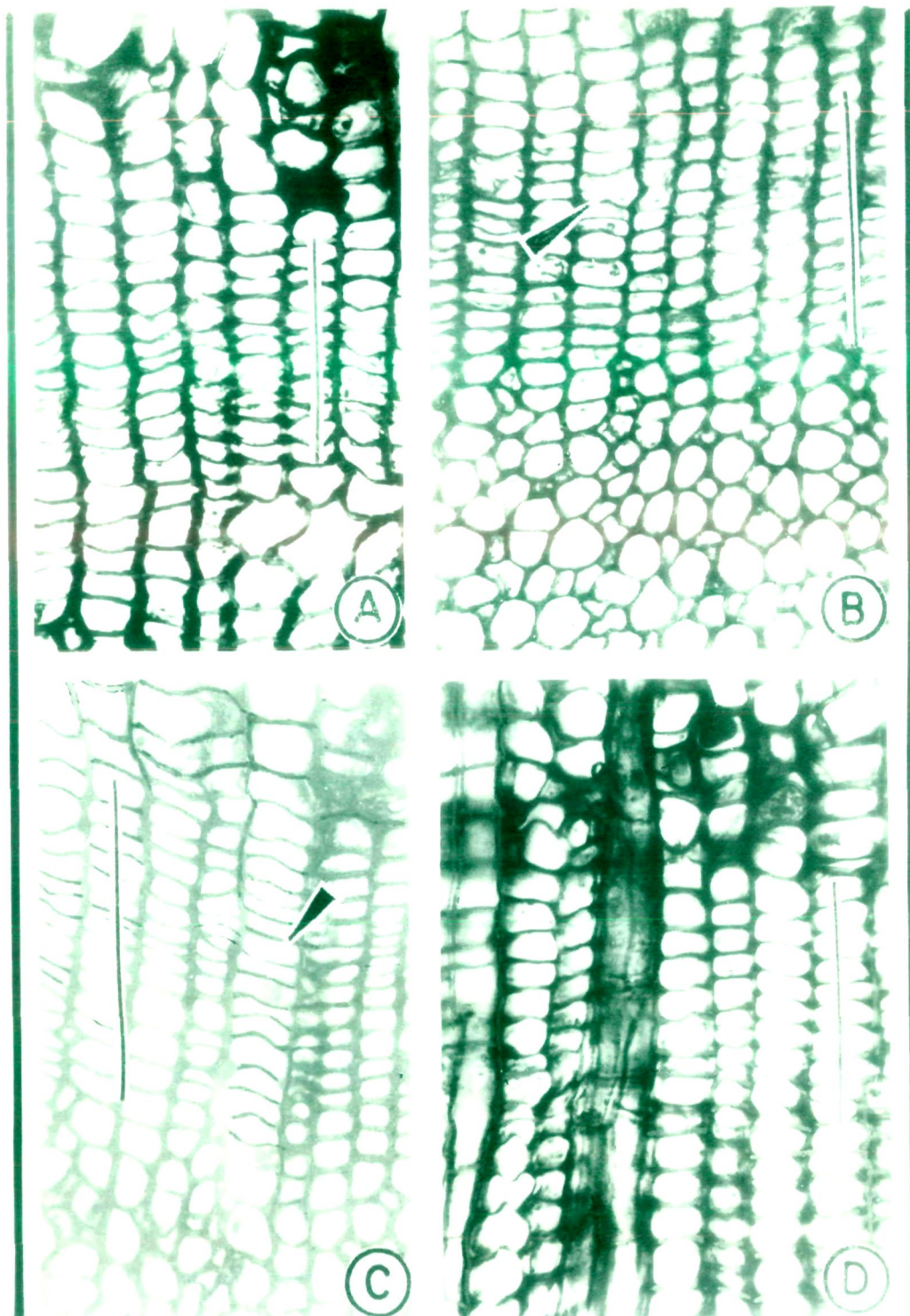


PLATE VIII

PLATE - IX. Structural details of conducting phloem in  
Acacia nilotica and Prosopis spicigera:

- (A-B) T.L.S. of Acacia phloem showing sieve-tube members (ST) and the associated elements. Compound sieve plates (SP) and the rows of sieve areas on lateral walls (arrow) can be seen. (Both at x600)
- (C) T.L.S. of Prosopis phloem showing sieve tube members (ST) and the associated elements. Compound sieve plates (SP) and the rows of sieve areas (arrows) can be seen. (x330)
- (D) T.S. of Prosopis phloem showing distribution of sieve-tube members (ST), companion cells (C), axial parenchyma (P) and radial rays (R). ( x600 ).

PLATE - X. Variation in structure of cambium and wood of  
Prosopis spicigera with respect to the relative  
age of the stem axis:

- (A) T.L.S. of cambium from young axis showing abundance of short, uniseriate ray initial units. ( x 190 )
- (B) T.L.S. of cambium from the main tree trunk showing widely spaced tall and broad ray initial units. ( x 150 )
- (C) Magnified view of the cambium in old axis. ( x 600 )
- (D) T.S. of wood from young axis showing fine rays, isolated vessels (V) and poorly lignified fibre cells. ( x 150 )
- (E) T.S. of wood from the mature tree trunk showing broader rays, vessels surrounded with paratracheal parenchyma (P) and fibres (XF). ( x 150 )

F.I. = Fusiform initials

P. = Parenchyma (axial)

R. = Ray initials

V. = Vessels

X.F. = Xylem fibres.



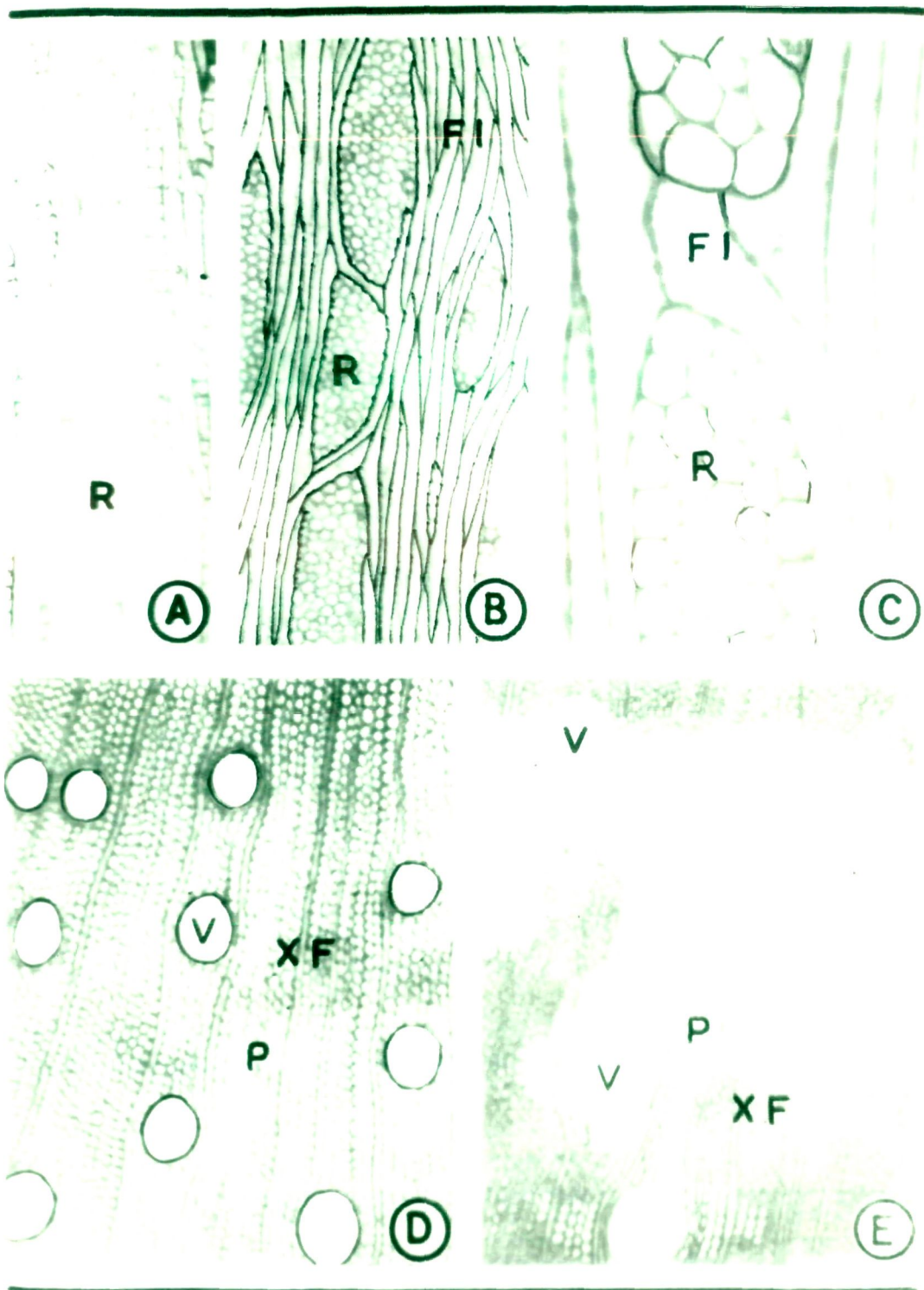


PLATE X

## APPENDIX - I

### LIST OF PUBLICATIONS OF MUHAMMAD IQBAL

#### Research Papers

1. A comparative study on the cambial structure of some arid zone species of Acacia and Prosopis. Bot. Notiser (Sweden), 128: 327-331, 1975 (with A.K.M. Ghouse).
2. Ratio of ray and fusiform initials in the vascular cambium of some arid zone plants. Curr. Sci. (India), 44: 361-362, 1975. (with A.K.M. Ghouse & M. Yunus).
3. Ray and fusiform initials in some Bauhinia species. Curr. Sci. (India), 44: 442-443, 1975 (with A.K.M. Ghouse & M. Yunus).
4. A comparative study on the cambial structure of some Bauhinia species. Bot. Jahrb. Syst. (F.R.G.), 95: 411-417, 1976 (with A.K.M. Ghouse & M. Yunus ).
5. Variation trends in the cambial structure of Prosopis spiciigera L. in relation to the girth of the tree axis. Bull. Torrey Bot. Club (U.S.A.), 104: 197-201, 1977 (with A.K.M. Ghouse ).
6. Ontogenetic size variation in vessel elements of Prosopis spiciigera L. Flora (G.D.R.), 166: 187-192, 1977 (with A.K.M. Ghouse ).
7. Trends of size variation in phloem fibres and sieve-tube

- cells within the bark of some arid-zone trees. *Flora* (G.D.S.), 166: 517-521, 1977 (with A.K.M. Ghouse).
8. Ontogenetic size variation of sieve-tube elements in Prosopis spicigera L. *Bull. Soc. Bot. Fr. (France)*, 124: 445-450, 1977 (with A.K.M. Ghouse).
  9. Cell length variation in the secondary phloem of some medicinally important tropical trees. *Ha-Yaaran (Israel)*, 27: 55-60, 1977 (with M. Yunus & D. Yunus).
  10. On the occurrence of styler heteromorphism in Solanum. *Ceylon J. Sci. Biol. Sci. (Ceylon)* 14: 1978. (with S. Baksh & M. Yunus).
  11. On the cambial structure of some industrially important tropical trees. *Flora (G.D.S.)*, 167: 159-163, 1978. (with M. Yunus & D. Yunus).
  12. Floral features of Solanum macranthum Dun. with special reference to styler heteromorphism and intercrossability. *Flora (G.D.S.)*, 167: 423-431, 1978 (with S. Baksh).
  13. Interspecific quantitative variation of active mass transfer medium in the main trunks of some arid zone Acacia and Prosopis. *Flora (G.D.S.)*, 167: 466-471, 1978 (with A.K.M. Ghouse).
  14. Surface imprinting by colloidal. *Micr. Acta (F.R.G.)*, 80: 353-357, 1978 (with M. Yunus & D. Yunus).
  15. Breeding system of Solanum integrifolium Poir. with an emphasis on sex potential and inter-crossability. *Euphytica (Netherlands)*, 27: 811-815, 1978 (with S. Baksh & A. Jamal).

16. A new report of environmental parthenocarp in Solanaceae. *Isr. J. Bot. (Israel)*, 27: 62-65, 1978 (with S. Baksh & A. Jamal).
17. Impact of anatomical research on some Botanical concepts. *Sci. & Environ. (India)*, 1: 5-10, 1979.
18. Compatibility relationships in some non-tuberiferous species of Solanum. *J. Hort. Sci. (England)*, 54: 163, 1979. (with S. Baksh).
19. Taxonomic significance of sclerenchyma distribution in the secondary phloem of some Indian tropical trees. *Feddes Repert. (G.D.R.)*, 90: 171-176, 1979 (with A.K.M. Ghouse, F. A. Siddiqui & A. Jamal).
20. Intrusive growth in the secondary phloem of Acacia and Prosopis. *New Bot. (India)*, 6: 1979 (with A.K.M. Ghouse).
21. An outline of the bark anatomy of some arid zone Acacia and Prosopis with particular attention on sclerenchyma distribution. *Geophytology (India)*, 9: 1979. (with A.K.M. Ghouse).
22. Studies on anatomical changes in Prosopis spicigera L. with growing girth of stem axis. *Phytomorphology (India)*, 29: 1979 (with A.K.M. Ghouse).
23. Styler heteromorphism and floral fertility in Solanum hispidum Pers. (Solanaceae). *Brenesia (Costa Rica)* 16: 53 - 59, 1979. (with S. Baksh).
24. Reproductive biology of Solanum elaeagnifolium L. and its compatibility relationship with egg-plant. *Bot. Jahrb. Syst.* in press, (with S. Baksh).



25. The vascular cambium and its activities in Indian trees: A review. Proc. Symp. "Progress of Botany during the last decade" Jaipur, in press, (with A.K.M. Ghouse).
26. Size of sieve-tube elements and age of the tree of Prosopis spicigera L. Proc. Symp. "Recent researches in Plant Sciences" Patiala, in press, (with A.K.M. Ghouse).
27. Need of interdisciplinary approach in the study of plant growth and development and their response to pollution hazards. Proc. Symp. "Interdisciplinary research, teaching and University administration", Aligarh, in press, (with A.Z. Amani, K.K. Khan & A.K.M. Ghouse).
28. A biographical memoir on Professor Rafil Ahmad Chowdhury (1902-1978) I.N.S.A. Publications, New Delhi, in press, (with A.K.M. Ghouse).
29. Comparative bark features of some arid zone species of Acacia and Prosopis (Mimosaceae). Phytomorphology, in press, (with A.K.M. Ghouse).
30. Anatomical features for the identification of isolated bark of some Bauhinia species. Bull. Soc. Bot. Fr., in press, (with K.K. Khan & Z. Ahmad).

### Abstracts

1. Proportion of functional and non-functional bark in Acacia and Prosopis. All India Symp. "Recent Advances in Plant Sciences", Kalyani, p. 116-117, 1976 (with A.K.M. Ghouse).
2. Variation in the amount of porous medium for the flow of soil solution in relation to the growing girth of the

- axis of an arid zone tree. All India Symp. "Flow through Porous Media", Pilani, Abst. 2.9, 1976 (with A.K.M. Ghouse)
3. Ratio of ray and fusiform initials in the vascular cambium of some tropical trees of India. 46th Ann. Sess. N.A. Sc. India, Rajkot, p. 7-8, 1976 (with A.K.M. Ghouse, F.A. Siddiqui & S. Hashmi).
  4. Size of sieve-tube elements and age of the tree of Prosopis spicigera. All India Symp. "Recent Researches in Plant Sciences", Patiala, p. 26, 1977 (with A.K.M. Ghouse).
  5. The vascular cambium and its activities in Indian trees. All India Symp. "Progress of Botany during the last decade (1965-1975)", Jaipur, p. 61-62, 1977 (with A.K.M. Ghouse).
  6. Bark anatomy of some arid zone species of Acacia and Prosopis. 2nd Indian Geophytol. Conf. Lucknow, p. 17, 1978. (with A.K.M. Ghouse).
  7. Acacia nilotica (L.) Willd. An ideal tree form of arid zone environment. International Symp. "Arid zone Research and Development", Jodhpur, p. 121, 1978 (with A.K.M. Ghouse).
  8. Studies on the bark of Prosopis spicigera L. with special reference to its thickness in relation to age of the trunk. 47th Ann. Sess. N.A. Sc. India, Bhopal, p. 34, 1978 (with K.K. Khan & A.K.M. Ghouse).
  9. An assessment study of evolutionary status of ray initials in some Indian tropical trees. 47th Ann. Sess. N.A. Sc. India, Bhopal, p. 32, 1978 (with A.K.M. Ghouse, F.A. Siddiqui & S. Hashmi).
  10. Variation in amount and magnitude of cambial initials at different levels of the stem axis of Acacia nilotica var. gulia. 48th Ann. Sess. N.A. Sc. India, Gauhati, p. 36,